Vol. 22 No. 7

July, 1956

THE BOTANICAL REVIEW

Interpreting Botanical Progress

Chromosomal Interchanges in Plants ..... C. R. BURNHAM 419

FUTURE CONTENTS
ON INSIDE BACK COVER

Published Monthly except August and September
Box 749, Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
EDMUND H. FULLING

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Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied without charge unless notice is received within two months after appearance of issues concerned.

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THE BOTANICAL REVIEW

VOL. XXII JULY, 1956 No. 7

CHROMOSOMAL INTERCHANGES IN PLANTS[1]

C. R. BURNHAM[2]

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General Information

INTRODUCTION

Individuals that are heterozygous for a rearrangement of segments of chromosomes show characteristic and usually predictable changes, both in chromosome behavior at meiosis and in their heredity. Such individuals have been referred to as " structural

[1] Contribution of the Department of Agronomy and Plant Genetics, University of Minnesota, Institute of Agriculture, St. Paul 1, Minnesota. Miscell. Journal Series No. 890, Agricultural Experiment Station.

[2] Prof. of Plant Genetics, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul 1, Minnesota.

hybrids". The rearrangements may be either within a chromosome, between members of a pair of homologues, or between non-homologues. They may result in inversions, insertions, duplications, deficiencies or interchanges. When the interchanged end segments belong to opposite arms of the two members of one homologous pair, pseudoisochromosomes result. The interchanges will be the main consideration of this review. They are the result of exchanges of segments of non-homologous chromosomes. They were first termed "segmental chromosomal interchanges", but are referred to now as interchanges, reciprocal translocations, or translocations. The change in which a piece of one chromosome is supposedly attached to the end of an unbroken chromosome has been referred to as a "simple translocation". The evidence is that these do not occur. Their absence may be due to the non-fusibility of intact chromosome ends, as first suggested by Stadler (1932). The change in which an internal segment has been inserted at another position does occur and has been termed an insertional or intercalary translocation.

The changes may have arisen "spontaneously", or as the result of experimental treatments. The evidence thus far is that all produce similar types. Studies which are primarily on the effects of experimental treatments are not included in this review. Interchanges which were produced in that way, established, and used for further studies are included. The review is confined mainly to plants, except for certain general facts and differences which apply to animals. A general discussion of interchanges is followed by a more detailed presentation for each species in which the interchanges or translocations have been found, arranged alphabetically by families.

The first observation of the attachment of more than two chromosomes to form a ring seems to have been by Gates (1908) in *Oenothera rubrinervis*. Cleland (1922, 1929) observed that the chromosomes in the ring in any *Oenothera* race are associated in a specific and constant order. Later the term catenation was used by Gates for chromosomal linkage. Digby (1912) observed that two chromosome pairs were joined together in a ring in the amphidiploid *Primula kewensis* ($2n = 36$). Sands (1925) saw the characteristic chains in *Tradescantia virginicus* and also in *Rhoeo*, but interpreted them in terms of the synapsis theories current at that time.

The first case suggested to be a structural change involving two non-homologous chromosomes was reported in *Drosophila melanogaster* by Bridges (1923). A dominant pale eye color (P), a specific diluter of eosin, was linked with factors in two chromosomes. It was interpreted as the association of Pale with a translocation of a piece of II to chromosome III, assumed to result in a branched chromosome. The new eye color was inseparably associated with the change, but was lethal in homozygous condition. After the salivary gland method of analyzing *Drosophila* chromosomes was discovered, Bridges (1934, 1936) reported that in the "Pale translocation", a non-terminal segment of II had been inserted in III. In 1937 he determined the length of the deficiency in II. The piece inserted in III may not have included all of the portion missing from II. Muller (1947) reported that the cause of the recessive lethal effect was not at or near the left break.

In plants, what later proved to be the first accounts of the breeding behavior of a probable case of interchange was by Belling (1914a, b, 1915a, b). While working on a breeding program for improvement of the Florida velvet bean (*Stizolobium deeringianum*), Belling reported sterility in hybrids between it and the Lyon, Yokohama and Chinese velvet beans[3]. Since he observed about 50% of aborted pollen and ovules, the condition was termed "semisterility". The progeny of these hybrids included semisterile and normal plants in 1 : 1 ratio. In the subsequent generations, the semisteriles continued to segregate in this manner, while the normals bred true. Linkages between semisterility and other characters were reported also. In the 1915 report he noted that he was dealing with gametophyte abortion and also proposed a two-factor hypothesis which would account for the breeding results, i.e., that the Florida velvet parent was *K l* and the others were *k L*, the *KL* and *kl* gametic combinations being abortive. Belling pointed out then that the abnormal behavior of two chromosome pairs would also explain the results. He predicted that the fertile progeny of semisterile plants should be of two types, such that when intercrossed they would give semisterile hybrids.

During the course of subsequent cytological studies, Belling found that the unexpected ratios for new phenotypic characters which Blakeslee was finding in *Datura stramonium*, the Jimson

[3] The Lyon bean is *S. niveum*; the Yokohama, *S. Hassjoo*.

weed, were due to the presence of an extra chromosome, i.e., they were trisomics. In one of these, which reoccurred only in crosses with a certain race ("B white"), a small chromosome was attached to two large ones. From this Belling concluded that one of them must have had an end from a non-homologue and that non-homologous chromosomes could exchange segments (Belling and Blakeslee, 1924). Belling (1925) then showed that in *Stizolobium* the semisterility and its breeding behavior could be explained as the result of "segmental interchange between non-homologues". Those reports included confirmation of the prediction that the normals in the progeny from selfing of semisteriles were of two types, the hybrids between them being semisterile. The evidence in *Stizolobium* was entirely genetic (Belling, 1928)[4].

Belling believed that semisterility would be found in the crosses with "B whites" in *Datura*. Workers at Blakeslee's laboratory found that those crosses did not give semisterile F_1's but that other crosses did. Belling had left, but they soon found rings and associations of four chromosomes in both types of crosses (Blakeslee, 1928), also confirmed by Belling (see Blakeslee, 1941, for a more detailed account).

Hammarlund (1923) reported in *Pisum* a close linkage between characters ordinarily independent. The association of four chromosomes in a ring in this material was reported by Håkansson in 1929.

The first cytological demonstration of a translocation, according to Muller (1929), was provided by Stern (1926) in *Drosophila*, a piece of the Y- having become attached to the end of the X-chromosome.

The first published application of Belling's hypothesis as an explanation of the rings in *Oenothera* seems to have been by Håkansson (1928). It had been applied at about the same time in a Ph.D. thesis at the University of Michigan by Sterling Emerson (1928b), the application having been suggested to him originally by Belling in a conversation. Darlington (1929) published a discussion of the application and expectations of the

[4] It should be pointed out here that the sterility and ratios given by a relatively long pericentric inversion (one break in each arm of a chromosome) would be similar. It differs cytologically, since only one chromosome pair would be included in the inversion configuration. A paracentric inversion usually shows pollen abortion but not ovule abortion.

theory. Cleland and Blakeslee (1930, 1931) applied it to certain crosses.

The first cytological demonstration of the location of an interchange between two non-homologous chromosomes in plants was by McClintock (1930) for a case of semisterility in maize[5]. The 4-armed figures at the pachytene stage of meiosis were drawn by camera lucida and measured to determine the points of exchange. This laid the foundation for extensive studies in maize, using chromosomal aberrations as tools in the study of cytogenetic problems (see the later discussion in this section on uses, pages 453-459).

Chromosomes referred to as "pseudoisochromosomes" were first reported by Caldecott and Smith (1952) in the progeny of X-rayed barley seeds. In place of each having two identical arms as with true isochromosomes, segments adjacent to the centromeres may not be homologous. These have been found in maize also (Morris, 1955), and their supposed morphology confirmed by the observed pachytene pairing.

GENERAL BEHAVIOR

CYTOLOGY, CHROMOSOME SEGREGATION. The general cytological and genetical behavior in diploids will be discussed first. They apply equally well to many allopolyploids which, although they have a higher chromosome number, still behave as diploids in many respects. Certain of the differences will be considered as we proceed. In individuals heterozygous for one interchange, two pairs of chromosomes are usually associated in a ring or a string or chain at meiosis. This group of four chromosomes[6] includes a

[5] In the summer of 1929, the writer grew at Cornell University the original semisterile line of maize reported by Brink (1927), and also two new lines (semisteriles-2 and -3) and their intercrosses. These new lines were found in a genetic stock being used at the University of Wisconsin. They had not been examined cytologically. McClintock had found at Cornell University a line that had an association of four chromosomes at meiosis. Examination of the pollen showed that line to be semisterile. Cytological examination of my semisterile lines showed them to have a ⊙4 (Burnham, 1930), thus connecting the separate observations. McClintock's 1930 paper was on semisterile-2. Rhoades' 1931, 1933 papers were on McClintock's semisterile line.

[6] In the literature, these are referred to frequently as quadrivalents or written as a IV. Since multivalents also indicate multiple homologues as in polyploids, these terms have been avoided for cases which appear to involve translocation or in which there is doubt.

normal and an interchanged member of each of the two pairs. The pairing of homologous portions results in a cross-shaped configuration observable at pachytene. At diakinesis and metaphase I of meiosis it opens up into a complex of four chromosomes associated mainly at the ends.

This quadripartite group of chromosomes may be oriented at metaphase I so that either alternate or adjacent chromosomes are directed toward the same pole, a zig-zag or an "open" configuration, respectively. For the adjacent segregations, there are two types, adjacent-1, in which the two chromosomes with homologous centromeres pass to opposite poles, and adjacent-2, in which they pass to the same pole. In the adjacent segregations there is nondisjunction for certain chromosome segments. For example, if the normal chromosomes are designated as 1 and 2, and the interchanged ones as 1^2 and 2^1, the superscripts indicating the pieces received[7] in the exchange, the order of the chromosomes in the ring is: $1 - 1^2$. If crossing-over is ignored, the results of the

$$\begin{array}{cc} | & | \\ 2^1 & - 2 \end{array}$$

three possible segregations at meiosis, considering only those receiving two chromosomes, are:

1. alternate: $1 + 2$ = standard normal; and $1^2 + 2^1$ = interchange, both chromosomes complete
2. adjacent-1: $1 + 2^1$ and $1^2 + 2$, = both deficient (also with a duplication)
3. adjacent-2: $1 + 1^2$ and $2 + 2^1$, = both deficient (also with a duplication)

Only the alternate segregation results in combinations that are not deficient. In higher plants the deficient spores usually abort. They are unable to complete the divisions and the development necessary to form the gametophyte. This results in pollen grains which are smaller than normal and appear to be empty or nearly so.

Hagberg (1954) recognized another type of orientation in which two chromosomes on opposite sides of the ring are directed to opposite poles, but the ones adjacent to them are not coorientated toward either pole. This may disjoin to give 2–2 or 3–1 segregation.

[7] The segments without the centromeres are considered to be the ones exchanged.

Ovule abortion shows up as undeveloped seeds. If the deficiency is a short one or for less-essential genes, the pollen may be partially filled or even appear normal, although usually non-functional. The same deficiency in the ovules may be functional. When such ovules function, in crosses with normal pollen, the resulting plants are trisomic for the duplicated segment.

In certain species, alternate chromosomes in the interchange complex pass to the same pole 70 to 90% of the time, while in others alternate and adjacent segregations are about equally frequent. In the former type, which is said to have directed segregation, ovule and pollen abortion are usually low [8]. Examples are *Oenothera, Triticum monococcum, T. durum,* and probably barley and *Datura.* In the other type, which does not have directed segregation, pollen and ovule abortion are usually about 50%. Examples are *Zea mays, Pisum sativum, Sorghum versicolor* and *Petunia.*

IDENTIFICATION OF HETEROZYGOTES. In higher plant species with completely directed segregation, the interchange heterozygotes would have to be identified cytologically by the association of two or more chromosome pairs at meiosis, or genetically by linkage between characters normally independent.

In polyploids, spores deficient even for large segments may not abort, because of the duplications present in other chromosomes. In spite of this, in such an interchange heterozygote, transmission of these types through the pollen may fail or be low as a result of the additional duplication resulting from adjacent segregations. Here also spore abortion cannot be used to identify the interchange heterozygotes.

In higher animals there is no intervening gametophyte stage between the end of meiosis and formation of the gametes; consequently gametes which arise from the adjacent segregations in an interchange chromosome complex are functional in spite of the deficiency they carry. If they unite with normal gametes, the resulting zygotes are heterozygous for a deficiency and also carry the accompanying duplication. They may die at various stages of development. Except in species with completely directed segregation, the interchange heterozygotes may be identified by a de-

[8] As will be shown later, crossing-over in an interstitial segment (between the centromere and an interchange break point) will produce some spore abortion, see p. 426.

creased egg-hatch, as used, for example, in *Drosophila* (Dobzhansky and Sturtevant, 1931; Pipkin, 1940; Brown, 1940), or a lower litter size, as used in mice (Snell, 1935, 1946; Koller and Auerbach, 1941; Hertwig, 1941). Abnormally developed lethal zygotes were noted in litters from translocation heterozygotes and supposed to be from unbalanced chromosome combinations (Snell, 1935). Linkage between characters normally independent has been used also in mice.

EFFECT OF CROSSING-OVER. In presenting the results of the three possible kinds of segregation as shown earlier, the effect of crossing-over was not considered. Crossing-over in the interstitial[9] segments gives results different from those after crossing-over in any of the other regions of the chromosomes in the interchange complex. The latter cross-overs merely transfer blocks of genes between the interchanged and the normal chromosomes. In contrast, when crossing-over in the interstitial segment is followed by alternate or adjacent-1 segregation, half of the resulting products of that meiosis (spores in plants, gametes in animals) are normal and half carry a deficiency + duplication[10]. In higher plant species with directed segregation, these cross-overs are a source of spore abortion. One with completely directed segregation should have normal pollen and seed set only if there is no crossing-over in the interstitial segments. These points are illustrated by showing the effects of crossing-over in an interstitial segment, using the notation on page 424. After crossing-over, the four pairs of chromatids might be $(1 + 1) \quad — (1^2 + 1^2)$

$$\begin{array}{cc} | & | \\ (2^1 + 2^{\text{c.o.}}) & — (2 + 2^{1\ \text{c.o.}}) \end{array}$$

Note: c.o. = cross-over

The combinations of chromatids in the four cells at the end of meiosis would be:

following alternate segregation: $(1 + 2)$ = normal;
$(1 + 2^1)$ = c.o., deficient;
$(1^2 + 2)$ = c.o., deficient;
$(1^2 + 2^1)$ = interchange.

[9] "Interstitial" as used here refers to the region between the centromere and the point of interchange. It has been applied also to chiasmata which are non-terminal.

[10] This was termed "half-disjunction" by Sansome (1933).

following adjacent 1 segregation: $(1 + 2)$ = c.o., normal;
$(1 + 2^1)$ = deficient;
$(1^2 + 2)$ = deficient,
$(1^2 + 2^1)$ = c.o., interchange.

There is evidence (McClintock, 1945, p. 675) that chromosomes that have crossed-over in an interstitial segment pass to opposite poles; hence adjacent-2 segregation would not be expected and is not shown above.

A further important point to be seen from the above presentation is that when such cross-overs are followed by alternate segregation, the cross-over chromatids are in the spores that are deficient and abort, but when followed by adjacent-1 segregation, the cross-over chromatids are in the spores that do not abort, either normal or interchange combinations. Hence in a species with all or an excess of alternate segregation, crossing-over is reduced in the regions included in the interstitial segments, due to abortion of the cross-over chromatids. Only certain multiple cross-overs within either segment, or simultaneous singles in both, would be recovered. Also it should be noted that in each such spore quartet the two deficient + duplication types are complementary to each other and are similar to the ones resulting from adjacent-1 segregation when no crossing-over occurs in the interstitial segments.

The above relations seem to have been recognized first by Darlington (1931a) and in 1939, also by Sansome (1932, 1933) and Sutton (1935). They were stated in still clearer terms by Marquardt (1941, p. 287), also by Parthasarathy (1940), Wanner (1941), Smith (1948), Tometorp (as given by Lamm, 1948), Hanson and Kramer (1949), Hanson (1950) and Burnham (1949, 1950b). They appear not to have been recognized in the *Drosophila* investigations on translocations previous to Novitski (1951). Muller (1930) mentioned the possibility that chromosome segregation in translocation heterozygotes might be different in the two sexes.

IDENTIFICATION AND BEHAVIOR OF HOMOZYGOTES, DEFICIENT GAMETES. In plants the above scheme of interchange with or without crossing-over in interstitial segments accounts for the ratio of 1 normal : 1 interchange heterozygote from crosses of normals with interchange heterozygotes. Selfs of the heterozygotes

or sib crosses between them give the same 1:1 ratio, but the normals are of two types, either standard or homozygous interchange. The latter have been identified by the fact that when crossed with a standard normal, the F_1 has an association of four chromosomes and is partially sterile in species without completely directed segregation. This test has been standard procedure in isolating lines homozygous for the interchanges in maize, *T. monococcum, Datura, Nicotiana* and barley. In maize it has been possible to establish homozygous lines in all but a few which are closely linked with a defective character. In barley no failure has been found thus far in segregating lines adequately tested. In *Drosophila melanogaster,* on the other hand, at least half of the translocations are not fully viable as homozygotes, the homozygotes being either completely lethal, semilethal or viable but sterile (based on a tabulation of the information in Bridges and Brehme, 1944). This is probably due to the lack of an effective gametophyte screen against deficiencies such as there is in higher diploid plants.

In animals the cross of two individuals heterozygous for the same translocation gives another result not expected in plants. In animals a deficiency + duplication gamete from one parent may unite with the complementary duplication + deficiency gamete from the other to produce a normal translocation heterozygote with all chromosome segments present. If in such a cross one parent is homozygous recessive, the other homozygous for the normal allele, recessives may be produced in F_1. This occurs when the duplication + deficiency gamete, which has the recessive factor duplicated, unites with the complementary type which is deficient for the normal allele. In *Oenothera* there is one report of recessives in F_1, but from the dominant-carrying translocation heterozygote crossed with the recessive not-translocated stock (Catcheside, 1954). Another was reported in maize by Gopinath (1950), but the female parent was heterozygous for two different translocations involving the same two chromosomes. In the latter case, a small deficiency, including the locus of the recessive, was probably viable and transmitted through the ♀ gametophyte.

3–1 SEGREGATIONS FROM INTERCHANGES. In addition to the regular segregations from the ⊙4 in which two chromosomes pass to each pole, irregular 3–1 segregations also occur, resulting in

(n − 1) and (n + 1) combinations. In higher plants the (n − 1) combinations abort. The (n + 1) pollen rarely functions in competition with normal pollen, but (n + 1) ovules do function to produce (2n + 1) or trisomic individuals which have one or both of the translocated chromosomes. Those with one translocated chromosome are called tertiary; those with both, interchange trisomics. In species not having completely directed segregation, these trisomics have lower degrees of sterility than the 2n interchange heterozygote, e.g., in maize their sterility is 15 to 30% as compared with the usual 50%. In *Datura* they show certain of the phenotypic characters found in two different primary trisomics. They have been reported in the progeny of translocation heterozygotes in maize by Burnham (1930), McClintock (1931a), Ibrahim (1950a, b); in *Pisum* by Sansome (1933), Nilsson (1936), Håkansson (1936b), Sutton (1939), Pellew (1940); in *Crepis* by Levitsky (1940), Gerassimova (1940b); in *Campanula* by Darlington and Gairdner (1937); in barley by L. Smith (1941), Burnham et al. (1953, 1954), Hagberg (1954), Ramage (1955); in *Nicotiana* by Goodspeed and Avery (1939); and in *Datura* by Blakeslee (1927a, b, 1931) and Belling (1927). They have been recognized in *Drosophila* also (Dobzhansky, 1930a; Glass, 1933, 1935).

LINKAGE DETERMINATIONS, EFFECT ON CROSSING-OVER

In those species in which the translocation heterozygotes may be identified by their partial sterility, linkage tests between the sterility and the genetic markers may be made. In species that are easily crossed, the partially sterile F_1 may be backcrossed to the recessive genetic stock, as in maize. In such crosses, the sterility behaves as a dominant character, segregating 1 normal: 1 partly sterile. For species not easily crossed, F_2 data may be used, also F_3. In F_2 and F_3 the normal offspring are of two types, those homozygous for the translocation and those homozygous for the standard normal condition. Special formulas are required for calculation of recombination. Recombination values have been calculated from F_2 data involving translocations in *Pisum* by means of maximum likelihood formulas (Pellew, 1940)[11], and in barley

[11] And others, see p. 472. Lamprecht (1953c) compared the results using the product and maximum likelihood methods.

by the product method (Joachim, 1947), and for F_2 and F_3 data by maximum likelihood but with a special transformation (Hanson and Kramer, 1950). The methods and formulas for calculation by maximum likelihood have been summarized by Kramer (1954). This includes derivation of the formulas. See also Kramer and Burnham (1947). Tables necessary for easy use of the product method have been published by Joachim (1947).

Belling (1915b) was the first to report linkage data between semisterility and other segregating characters. On the basis of the interchange hypothesis, semisterility should show linkage with factors in two different linkage groups. This was first reported for an interchange by Brink and Cooper (1931) in maize. Linkage between factors in the two linkage groups involved in the translocation would also be expected and was first reported by Rhoades (1931, 1933) in maize.

In the homozygous translocation stock, genes on opposite sides of the break in either of the two original chromosomes are no longer linked, while genes not previously linked but in the two chromosomes translocated may now be linked. Examples in maize have been reported by Anderson (1941), Anderson and Randolph (1945), Patterson (1952), Anderson and Kramer (1954), Anderson, Kramer and Longley (1955a, b). Certain linkages are found only in the translocation heterozygote and are due to the sterility of the non-parental combinations of chromosomes. These are pseudo-linkages.

In general, crossing-over is greatly reduced in regions near the breakage points, e.g., maize (Burnham, 1934b; Anderson, 1934). In maize this reduction seems to be attributable, at least in part, to the variable and non-homologous pairing in regions near the breaks (Burnham, 1934b). In T5-9a, the region of reduced crossing-over seems to be confined to the region with variable pairing (Burnham, unpublished). In this same region, crossing-over was much higher in the pollen than in the ovules, both greatly reduced as compared with that in normal plants (Burnham 1949b). Anderson, Kramer, and Longley (1955a) reported that translocations in the proximal portion of the short arm of chromosome-4 in maize did not suppress recombination, while those in the proximal portion of the long arm of that chromosome did. They suggested that the greatest suppression may be in heterochromatic regions proximal to the centromere.

In maize, both alternate and adjacent segregation are frequent after crossing-over in an interstitial segment (Burnham, 1953). Reduction of crossing-over due to the type of segregation is expected only if there is a much higher frequency of alternate than of adjacent-1 segregation. Reduced crossing-over in an interstitial segment, probably resulting from a high frequency of alternate segregation, has been reported by Hanson and Kramer (1950) and Hanson (1952) in barley. Reduced crossing-over has been observed in *Drosophila* translocations in the arm with the break; but some increase may occur in the other arm (Dobzhansky, 1933; M. S. Brown, 1940; Beadle, 1933; Pipkin, 1940). Dobzhansky (1931, 1932a, 1933) suggested competition in pairing as an explanation for the reduced crossing-over.

Rhoades (1931) reported no interference across the translocation point in a translocation heterozygote in maize. Data supporting this conclusion may be found in papers by Anderson and Kramer (1954), and Anderson, Kramer and Longley (1955a, b).

ORIGIN

Translocations may occur spontaneously, or in response to irradiation or treatments with certain chemicals. They may occur in somatic tissue or during meiosis. Some of the possible ways in which they may arise are presented here. Only a few of the possible citations are given.

1. Crossing-over between duplicated segments which are present in non-homologous chromosomes will produce translocations (Kihara and Nishiyama, 1937; Lamprecht, 1952; Kostoff, 1939b). Müntzing (1934) has discussed the effects of such cross-overs also. Kostoff (1941a) observed some pairing in *Nicotiana* haploids, and the presence of cross-over chromosomes in their diploid offspring. See also *Triticum* (p. 505).
2. The spontaneous association between heterochromatic regions could result in exchanges (Kostoff, 1938). Kostoff (1939d) suggested that such exchanges might account for the origin of cancer, variegations and irregular growth.
3. The interlocking of bivalents at meiosis appears to give an opportunity also for naturally occurring exchanges (Sax and Anderson, 1933). They observed interlocked bivalents in all diploid tradescantias examined, in 20% of the pollen mother

cells in *T. bracteata,* and in 15 and 40 per cent in two other species.

4. Accidental entanglement of chromosomes offers opportunities for interchanges as well as other changes (Darlington, 1931b).
5. They may result from chromosome breakages which are followed by the reunion of broken ends. These breakages may occur spontaneously or in response to external agents. Spontaneous breakage of univalents at their centromeres, i.e., misdivision, may lead to translocation if the pieces reunite in new combinations (Morrison, 1954, in wheat). Jones (1937, 1938) has presented genetic evidence that exchanges may occur between non-homologous chromosomes during the development of the endosperm in maize. McClintock (1941) reported spontaneous alterations in the chromosomes, one type being the result of crossing-over between the centromere and the nucleolus organizer in chromosome 6 in maize. She has reported spontaneous breakage and fusion also (1950, 1951). The locations of the breaks in these spontaneous translocations were not at random. At least one of the breaks was more likely to be at a pycnotic knob or at a centromere. Haga (1953) shows one figure in which there had been an interchange between the chromatids of two bivalents. Navaschin in 1926, 1928, 1931, 1934 also reported and discussed spontaneous changes in the chromosomes, some of which were translocations. Giles has reported spontaneous chromosome aberrations in *Tradescantia.* In 1940 he stated that the localization of spontaneous breaks in regions proximal to the centromere and the greater frequency of chromatid than chromosome breaks observed in *Tradescantia* suggest that they arise as the result of torsional strains associated with relic and relational coiling in the chromosome cycle. The rate was reported to be higher in 3n than in 2n or 4n plants (Giles, 1941). See also Darlington and Upcott (1941). L. V. Morgan (1939) reported a spontaneous somatic exchange in *Drosophila,* and Burkart (1931) a spontaneous translocation associated with light body color.
6. Translocations have been detected in the progeny of plants homozygous for the "sticky chromosome" character in maize (Beadle, 1937).

7. Interchanges have been found in plants grown from aged seed in wheat, both the 21 II and 14 II varieties, and also in barley (Gunthardt et al., 1953).
8. Translocations have been produced by certain chemicals (Auerbach, 1951); and in large numbers by X-rays, thermal neutrons and other irradiations (e.g., Anderson et al., 1949; Longley, 1950; Caldecott and Smith, 1952; Caldecott et al., 1952).
9. Treatment of maize pollen with ultra violet light has been reported to produce chromosomal changes, but deficiencies are more frequent than translocations. Reciprocal exchanges of segments were rare (Stadler, 1941; Singleton and Clark, 1940). Barton (1954) recorded interchanges following ultra violet irradiation of tomato pollen.

METHODS OF IDENTIFYING THE CHROMOSOMES INVOLVED

Summarized here are the methods of identifying the chromosomes involved:

1. The different interchanges may be intercrossed and the F_1's examined cytologically at meiosis. A $\odot 6$ indicates that one chromosome involved in the two interchanges is the same; $2\odot 4$ indicate that the two chromosomes involved in one are different from those involved in the other. If the same chromosomes are involved; only pairs or a $\odot 4$ will be observed, depending on whether the breaks are at similar, or at very different positions. This method has been used in maize (Burnham, 1930, 1934a; Anderson and Clokey, 1934; Anderson, 1935), in barley (Burnham et al., 1948, 1953, 1954), in *Triticum monococcum* (Yamashita, 1951), in *Pisum* (Sansome, 1937) and in *Datura* (Bergner and Blakeslee, 1943).

   Based on the intercross results, a tester set may be selected by which the chromosomes in any new translocation may be identified in terms of those in the tester set. One was established early in the work with maize and in the later work with barley (Burnham et al., 1954). In *Pisum* the intercross results on which selection of a tester set might be made have been reported (Sansome, 1937, 1938).
2. In maize most of the trisomics were available when the translocation work was started and the linkage group carried by

each was being determined by McClintock. By crossing the known (2n + 1) lines as ♀ with the translocation, cytological examination of the F_1 determined whether the extra chromosome was one of those in the ring—it was then a chain of five chromosomes; or whether it was a different one—the configuration then was a ⊙4 + III (Burnham, 1930). This identified the chromosomes of the translocation tester set with the linkage groups they carried.

3. In case trisomics are not available, linkage tests may be made between partial sterility and genetic markers in the different linkage groups as mentioned earlier. In those species in which the rings show no sterility, the plants in the linkage test would have to be classified cytologically as having a ⊙4 or only pairs. The other possibility is to test simultaneously for the segregation of factors in at least two linkage groups; the more groups tested the better the test. This has been used in *Drosophila,* but the lack of crossing-over in the male has greatly simplified the tests. The principle in tests of heterozygous females, as stated by Dobzhansky (1932a, p. 243), is that the gene closest to the one breakpoint will show the strongest linkage with the genes closest to the other breakpoint.
4. Cytological study at pachytene has been used to identify a large number of interchanges in maize (Longley, 1950). This identifies the chromosomes involved and the positions of the translocation breakage points. Certain chromosomes of maize are more difficult than others to distinguish. If the interchanges identified in this way are to be used for special studies, identification of the chromosomes should be carefully checked by this and by other methods.

   The salivary gland analysis in *Drosophila* has been used for the same purpose (e.g., Kaufmann, 1946).

INTERCHANGE TYPES, STERILITY, PACHYTENE BEHAVIOR, AND BREAKAGE POSITIONS

If the interchanged pieces are long, the configuration at pachytene of meiosis is 4-armed, or cross-shaped, the two translocated arms alternating with the centromere-bearing remainders of the two chromosomes. Supposedly, if a cross-over has occurred in each of the four arms, the configurations at diakinesis

and metaphase I will be rings. If one long piece has exchanged with a very short one, rings will be rare or non-existent, the metaphase I configurations being chains, the pachytene ones T-shaped [12]. If both pieces are short, rings may not occur or may be rare; chains may be most frequent, but two " pairs " will be common also. Examples of the latter in maize are T3-6 (Clarke and Anderson, 1935) and T5-9a (Burnham, in ms.). Cases have been observed in which an occasional chain configuration is the only evidence of the presence of a translocation (Burnham et al., 1954, in barley). McClintock (1934) reported a much lower percentage of ring configurations in a T6-9 interchange in maize when chromosome 6 was heterozygous for a modified satellite than when it was homozygous for the normal condition, indicating that relative arm length may not always be the controlling factor.

As another example, the frequency of ring configurations in T5-6c heterozygotes was considerably higher when chromosome 5 was normal than when it was homozygous for a pericentric inversion which decreased the length of the interstitial segment. In both cases, the relative arm lengths of the cross-shaped pachytene figures remained the same (Burnham, 1950; Khan, 1955).

In species with very short chromosomes, or with a low crossover frequency, a translocation may be present but not indicated by any observable associations of more than two chromosomes. This may be true for certain of the cases of sterility in *Galeopsis* (p. 469).

In maize, spore abortion is about 50% when both pieces interchanged are long, the usual configuration being a ring of four chromosomes. In several translocations having only chain configurations, spore abortion was 20–25% (Burnham, 1932a, 1950a). In these, one of the pieces exchanged was very short, and deficiency for it did not cause abortion. In the former report this duplication plus small deficiency was shown capable of functioning in the ovules and of giving fully viable plants. Similar behavior was found by Patterson (1952) in several maize translocations.

In one case of low sterility reported by Brink and Cooper

[12] T-shaped configurations have been interpreted as being the result of " simple " translocation. In two cases of such configurations in maize, an exchange of parts had occurred without question, since the short translocated piece was the end of the satellite (Burnham, 1932; Clarke and Anderson, 1935). Therefore T-shaped configurations are not conclusive evidence for simple translocation.

(1932a), the cross of low sterile ♀ × normal ♂ gave a ratio of 1 low sterile : 1 high sterile : 1 normal. The high-sterile class was hyperploid but had the normal chromosome number. The high sterility was due to a high frequency of 3–1 segregation in those plants.

In other translocations in maize, deficiency for a short piece results in smaller pollen which is filled with starch (Burnham, 1950b). In one such case a variable proportion of aborted and small but filled pollen grains was observed (Clarke and Anderson, 1935). If both pieces are very short, the pollen might be normal or nearly normal in appearance. Shortness of the deficiency is undoubtedly not the determining criterion, rather it is the physiological effect when the genes are missing.

The average sterility of the interchange heterozygotes in barley is 25% (White and Burnham, 1948; Burnham et al., 1954). Hanson and Kramer (1949) have pointed out that this indicates a high proportion of alternate segregation of the chromosomes in the ring. The amount of sterility in a species having only alternate segregation depends on the amount of crossing-over which occurs in the interstitial segments. It could approach 50% if those regions were long (Burnham, 1949, 1950b).

At pachytene in maize the center of the "cross-shaped" pairing configuration may be variable in position, and therefore may not always indicate the true break positions. In certain interchanges the position of the cross is less variable than in others (e.g., T8-9a, Burnham, 1934a). The variability may extend to both sides of the centromere (e.g., T2-6a, Burnham, 1932b), or in others only on one side of the centromere (e.g., T5-9a, Burnham, in ms.). There may be considerable asynapsis near the center of the "cross" (e.g., T1-7a, Burnham, 1948a), or there may be close pairing at all positions. In the latter there must be an association of non-homologous parts in those configurations with the "cross" not at the true break positions (McClintock, 1932; Burnham, 1932b). Darlington (1937) has considered this to be torsion pairing and not true pairing. There is evidence that crossing-over may occur in these non-homologously paired regions (Rhoades and McClintock, 1935; Stadler, 1935).

As already mentioned, in those higher plant species showing directed segregation, a translocation heterozygote may have normal

pollen or a low degree of sterility, the amount dependent, at least in part, on the frequency of crossing-over in the interstitial segments.

One possible type of translocation might be termed progressive or cyclical, pieces of three different chromosomes being transposed between the three so that each has taken its position in a new chromosome, replacing one of the other two, but none of them a reciprocal exchange [13]. Crossing-over could not separate these translocations. One of this type, but involving only two chromosomes, has been listed for *Drosophila,* T(2:3)109 (Bridges and Brehme, 1944, p. 197).

Translocations may occur between supernumerary chromosomes and members of the normal set. For example, in maize translocations between the supernumerary " B " type and primary "A", chromosomes have been reported by Roman (1942, 1947).

There are cases also in which two separate rings of four chromosomes are interdependent, so that they produce only two viable combinations of the chromosomes in the rings in place of the four expected if independent, for example, *Oenothera* (Emerson, 1935, 1936) and *Campanula* (Darlington and Gairdner, 1937). If one of the chromosomes in a ⊙8 carries a segment which is a duplicate of a segment in a chromosome opposite it in the ring, crossing-over will produce two new translocated chromosomes complementary to each other. If these go to the same pole, a viable combination with other chromosomes in the ring is possible, which, when combined with one of the gametes normally produced by the ⊙8, will result in the 2⊙4 which will form only two viable spore combinations (Burnham, unpublished). The necessary duplication without any accompanying deficiency may have arisen by two successive interchanges involving the same two chromosomes if the breaks are in the proper positions relative to each other (Gopinath, 1950; Gopinath and Burnham, 1956; Borojevic, 1954). Darlington and Gairdner (1937) suggested that the duplication arose by " redundant translocation ", supposing a deficiency was also present but no explanation was given.

The translocation breaks may occur at any point along the chromosome. For example, in maize they have been observed in

[13] Muller (1954) has described this as " translocation by triple exchange of a rotational nature ".

pycnotic regions (Creighton, 1934; Roman, 1947); in the satellite (Burnham, 1932a; Clarke and Anderson, 1935); in the nucleolus-organizer (Anderson, 1934; McClintock, 1934), dividing it into two parts which could form separate nucleoli; and in the centromere, dividing it into two functional halves (McClintock, 1931b). The latter was not an interchange, but does indicate another possible type of breakage which may precede interchange.

There is evidence that translocations in maize may not occur at random along the length of the chromosome, but in general the frequency is proportional to length (Anderson, 1935; Longley, 1950) [14]. In *Drosophila* breakages are much more frequent in heterochromatin than in euchromatin (see summary by Muller (1954), p. 377-380).

PHENOTYPIC EFFECTS ACCOMPANYING INTERCHANGES

In *Drosophila* the transposition of chromosome segments to new positions appears in some cases to be inseparably associated with phenotypic changes. The phenomenon has been termed " position effect ". For reviews on this subject, see Ephrussi and Sutton (1944), Muller (1954, p. 380-383) and Lewis (1950). In plants one case which appears to be well established is that reported by Catcheside (1947) in *Oenothera,* in which the translocation of a segment carrying a factor for broad red calyx stripes to a new position resulted in variegated patches of red. When the locus was transferred back to the normal chromosome by crossing-over, the normal phenotype was restored.

In maize, studies of homozygous translocations to test for the presence of such effects have been reported by Brink (1932) and by Roberts (1942). No conspicuous new characters were detected, but the latter found some small though significant differences in certain quantitative characters. Jones (1944) presented evidence that outgrowths on the surface of mature kernels of maize resulted when certain regions of chromosome 5 came into contact with others as the result of translocation. In *Datura,* Blakeslee et al. (1940) have stated that in their collection of over 90 prime types (homozygous chiefly for segmentally interchanged chromo-

[14] As analyzed in the latter report, the overall χ^2 comparisons were highly significant, but large deviations for one chromosome in the "A" bomb tests, and for two chromosomes in the X-ray tests accounted for more than half the total χ^2 values.

somes), most were not distinguishable from normal plants. For the few that were distinctly abnormal, they could not determine whether this was due to completely linked genes, deficiency at the break points, or to position effect. The studies of McClintock (1951, 1953) and Brink (1954) indicate a possible mechanism for "position effects". The shifts in position of an unusual kind of gene element which bring about phenotypic changes in known characters suggests some sort of insertional or intercalary translocation or transposition.

INTERCHANGES IN NATURAL POPULATIONS, SPECIES WITH LARGE RINGS

Translocations offer one method of accounting for interspecific sterility, by means of which divergent groups might be established, the hybrids between them being partially sterile and thus at a handicap (Sturtevant, 1938). In certain species, e.g., *Drosophila,* inversion seems to be a more frequent mechanism, although *D. pseudoobscura* and *D. miranda* do differ by several small translocations (Dobzhansky and Tan, 1936). As discussed by Darlington, 1939 (with certain modifications), the behavior of interchanges in natural populations depends on whether the species is self- or cross-pollinated, the size of the interchange, and the degree of sterility present in the interchange heterozygote in relation to the propagating potentialities of the species (i.e., its "margin of safety"). If the interchange heterozygotes show considerable sterility and have a small "margin", they are not likely to survive in a cross-pollinating species. They may become established as homozygotes in a self-pollinated species. If they are in a species in which the heterozygotes show high fertility (directed segregation), the interchanges may float in a cross-pollinated species, or again may be established as homozygotes in a self-pollinated one. If, as the interchanges float in a cross-pollinating species, they happen to pick up combinations which show heterosis, they may spread. They may also come to carry lethals which prevent their becoming homozygous. This latter phenomenon appears to have occurred in *Oenothera,* followed by an increase in the size of the ring by adding more interchanges. Races of *Oenothera* have become established in nature which are self-pollinated and in which all the chromosomes ($2n = 14$) are associated in a large ring at

meiosis. The segregation is largely alternate, resulting in the production usually of only two gamete types. They are nearly true-breeding because of the presence of balanced lethals or lethals of various types. Thus they are able to perpetuate any heterosis which is present. Stinson and Steiner (1955) also have stressed the selective advantage of the big ring in maintaining the hybrid vigor shown by the heterozygote, the bigger the ring the greater the likelihood of permanence of the heterozygosity in subsequent generations. Lethal or deleterious mutations would occur from time to time giving a further selective advantage to the heterozygote.

The types which survive may be influenced also by reproductive potential. In species with a low potential there is a lower margin of safety. Wright (1941) has discussed the fixation of translocations also. Also consult Stebbins (1950).

Other examples of true-breeding species with large rings are *Gaura biennis* (Bhaduri, 1942b) and *Rhoeo discolor* (Darlington, 1929a; Anderson and Sax, 1936). Others with large rings are *Hypericum punctatum,* which is probably true breeding (Hoar, 1931) and *Chelidonium majus,* with no information on breeding behavior (Nagao and Saki, 1939). In *Clarkia* (*Godetia*), certain plants in the wild races have large rings, and there is some evidence that a system of balanced lethals is gradually being established in nature (Håkansson, 1942; Hiorth, 1942b).

Certain *Paeonia* species have large rings but they seem to have no survival value, being long-lived perennials (Walters, 1941, 1942).

In *Campanula persicifolia,* a cross-pollinated, largely self-sterile species, the naturally occurring rings are not large, but under enforced crossing they seem to have accumulated lethals or other unfavorable genes in regions of the chromosomes near the interchange break points. These genes prevent survival of the homozygous types in the progeny produced by self-pollination. The self-sterility is an aid to maintenance of the interchange heterozygotes until a balanced lethal mechanism is developed (Darlington and Gairdner, 1937). In the wild, this results in a highly heterozygous breeding population. In a species such as this one with a high seed potential, estimated at 2,000 to 20,000 per plant, survival is possible in spite of a high frequency of deleterious genes or low fertility.

Surveys of isolated geographic races have been made in a few species by crossing with a standard line. In *Datura* such a check has shown that translocations have become established and may have been of some importance in the evolution of that genus (Bergner, 1943a, b; also see p. 486). In maize, a similar check by Cooper and Brink (1937) and by Rhoades and Dempsey (1953) has shown that naturally occurring translocations are rare in that species. According to the latter study, inversions are rare also.

DIFFERENCES IN KARYOTYPES IN RELATED SPECIES

There are also many cases in which related species show differences in chromosome morphology, many of which may be the result of translocation. Some may be the result of inversion or other changes. Those in which interspecific crosses indicate probable translocation have been included with the descriptions by families. No attempt has been made to assemble the literature, but a few examples are mentioned here. Stebbins (1950) should be consulted for a nearer complete presentation. The somatic sets of 14 populations of four species of the genus *Holocarpus* of the tarweeds show differences in morphology and number, not only between species but also between populations of the same race (J. Clausen, 1951). It was assumed that the differences may have come about through interchange of chromosome segments

Dark (1936) described the situation in two species of *Paeonia* in which many of the chromosomes in the somatic cells of the root tip did not have a morphologically similar partner. Two such chromosomes were found in two varieties of *Tulipa gesneriana* ($2n = 24$) (Upcott, 1937). Camara and Coutinho (1939) observed considerable variation in the chromosome idiograms of eight tetraploid wheats, and suggested rearrangements which would originate translocations and other changes.

Other examples of species in which translocation has been suggested as one cause of differences in karyotypes may be cited. Haga (1937) described differences in chromosome morphology in six karyotypes of *Paris hexaphylla* and suggested "simple translocation" as a possible cause. Kihara and Yamamoto (1931) described many kinds of karyotypes in *Rumex acetosa* and *R. montanus*. D. Love (1942) found a difference in morphology of one of the X-chromosomes in an intersex in *Melandrium rubrum*, and assumed that a piece of the Y had been translocated to it.

Sato (1936b) reported three different chromosome numbers in *Scilla ughii* (2n = 17, 19, 22). In *Scilla permixta* (Sato, 1936a) and in *Aloe* and *Gasteria* hybrids as well as *Haworthia* (Sato, 1937), differences in the satellite or in its location were described. Sinoto (1929) described a tripartite chromosome complex in *Humulus japonicus* and a quadripartite one in *H. lupulus*. In the latter the two end chromosomes were smaller and differed from each other. In *Muscari plumosum* a tandem satellite was found on one chromosome pair (Srinath, 1942), suggested as the result of a translocation involving two satellited chromosomes. In *Crepis* Swezy (1934) detected new positions of the satellite in occasional cells, and in 1937 reported a V-shaped chromosome in place of a rod in some of the cells. Lewis and Lewis (1955) suggested that part of the sterility in interspecific crosses in *Clarkia* may be caused by translocations not revealed by the pairing relations, this being the result of decreased chiasma frequencies.

EXPERIMENTAL PRODUCTION OF LARGER RINGS

Since certain natural species have evolved rings which include all or most of the chromosomes, it should be possible to build them experimentally, either by intercrossing translocation stocks or by successive X-ray treatments. In *Campanula* larger rings were built by intercrossing different lines and then selecting plants with the larger rings for further intercrosses (Gairdner and Darlington, 1931; Darlington and Gairdner, 1937). They state: "We have therefore obtained the higher rings in *Campanula* by successive backcrosses to plants having the interchanges of opposite parents so as to extract the interchanges from both sides of the ring" (Darlington and Gairdner, p. 102).

It has been demonstrated in maize that cross-overs in the differential segment (the region between two translocation breaks in the same chromosome) may occur rather freely and that they can be recovered (Burnham, 1946, 1953; Brink and Cooper, 1935). One goal of current work at the writer's laboratory in maize is to build a translocation stock which will produce a ring of 20 chromosomes when crossed with a standard normal stock, the hope being that this "Oenothera method" may be of use in practical breeding, e.g., in maize or barley (Burnham, 1946). One plan is to build the large ring by a series of crosses between

interchanges selected for their long differential segments, first to produce permanent ⊙6 combinations, then by inter-crossing them to produce a still larger ring. Crossing-over in differential segments is necessary to add the additional interchanges. A ring of six built by inter-crossing should have one differential segment; a ring of eight, two; and a ring of fourteen should have five such segments, or possibly more, as pointed out by Darlington (1932). A ring of 20, as planned now, may have six differential segments, with one chromosome made up of parts of four different chromosomes. In another plan, homozygous translocation stocks have been X-rayed. The largest ring of that type thus far is one with ten chromosomes (Burnham, unpublished). This was obtained in successive steps: first a ring of eight was produced by X-raying a stock homozygous for one interchange; then a line homozygous for the interchanges in the ⊙8 was X-rayed to produce lines which differed from it by one translocation. One of these homozygous lines produces a ⊙10 when crossed with a standard normal stock.

Yamashita (1951) has produced a ring including all the chromosomes of *Triticum monococcum* (a ⊙14); but both parents of the cross contribute interchanges.

Nishimura, Niizeki and Sato (1952) and Nishimura and Kurakami (1953) have reported the production of larger rings in barley by successive X-ray treatments in a scheme to produce the stocks for applying the *Oenothera* method of breeding to barley. They suggest that a stock which will give a ⊙8 + ⊙6 or a ⊙10 + ⊙4 in crosses may be more usable than the one with a complete ⊙14. The following is the plan they outlined. From several ⊙4 produced by the first treatment, the homozygous translocations are established. These are then X-rayed to produce further translocations. By crossing with standard normal types, they determine whether the new and the previous translocations have one or more chromosomes in common or none. Those lines which give a ⊙6 on crossing with normal are selected, and then pairs of lines which give ⊙6 + ⊙6 when crossed with each other are selected. The homozygous interchange stock from each ⊙6 line is to be established, and one of each pair of independent ⊙6 lines would then be given the third X-raying to produce a ⊙8 which when crossed with the other line member of the pair would give

⊙8 + ⊙6. In the 1953 report they had 14 lines with a ⊙4, two lines with a ⊙6 and the one with ⊙4 + ⊙4. Seven of those with a ⊙4 and the two with a ⊙6 and the one with 2⊙4 had been established in homozygous condition. They determined the fertility of the plants having rings of various sizes obtained from the intercrosses. Those with 2⊙4 = 45–48%; ⊙6 = 42 and 46%; ⊙8 = 26 and 30%; ⊙6 + ⊙4 = 29%. From these figures the average fertility of the desired ⊙8 + ⊙6 was calculated to be .28 × .44 or about 12%. They recognize the fact that in such a stock there would be two more arms without translocations than in one which would give a complete ⊙14. They also recognize that those with short translocated pieces would be more efficient in avoiding the undesired cross-overs between the translocation stock and the stock with which it is crossed.

FACTORS WHICH AFFECT SEGREGATION FROM RINGS

Why the rings in certain species should show directed segregation, while those in others do not, is still not satisfactorily explained. At least there appear to be exceptions which have not been resolved.

The species which show a high frequency of alternate segregation of the chromosomes at meiosis tend to have certain cytological features in common: the chromosomes are relatively uniform in length, the centromeres are median or nearly so, and the chiasmata are located at the ends or terminalize completely, e.g., *Oenothera, Rhoeo* and *Datura.* All of these features are true for the *Oenothera* rings which have survived in nature. The alternate segregation seems to be a characteristic not only of the larger rings in *Oenothera* but also of the ⊙8, ⊙6 and ⊙4 which are found in certain races.

Catcheside (1954) has reported mostly alternate segregations for a ⊙4 in *Oenothera blandina* with very unequal interchanged segments, produced by X-rays. Hence equality in length of the chromosomes in the interchange complex is not a necessary feature.

Gairdner and Darlington (1931) noted in *Campanula* that nondisjunction was more frequent in rings with non-terminal chiasmata at metaphase. In *Tradescantia edwardsiana,* Sax and Anderson (1933) reported a relationship between the kind of segregation from the ring and the relative frequencies of terminal and

subterminal chiasmata in the interchange complex. For configurations with only terminal chiasmata there was a ratio of about 2 alternate : 1 adjacent; for those with one subterminal chiasma it was 1 : 1.2; with two it was about 1 : 1.8; and with three subterminal chiasmata all segregations were adjacent (12 figures). When considered as a whole it was about 1 : 1. Pollen counts showed 45.6% of imperfect pollen.

In *Notonia grandiflora,* Ganesan (1939) observed that only 48% of the orientations in an association of four chromosomes were alternate, yet the chiasmata were mostly terminal. The unexpected behavior was attributed to the heterobrachial morphology of the chromosomes, i.e., the centromere position was toward the end of the chromosome.

Lawrence (1931) reported that in *Dahlia variabilis* (8x = 64), which is genetically a " double auto-tetraploid ", there is complete terminalization of all chiasmata. Certain of the chromosomes have a terminal centromere, others a median one. The very high percentage of good pollen and high seed germination, the latter as high as 100 per cent, were taken as evidence of normal chromosome segregations. Direct cytological observations are needed, since deficiencies usually are viable in a polyploid. Darlington (1937) has referred to differences in disjunction between tetraploid *Hyacinthus* in an association of four with interstitial chiasmata and in tetraploid *Primula sinensis* without such chiasmata. The former showed alternate and adjacent orientations, the latter had a high proportion of alternates.

An exceptional case with high terminalization, yet an equal frequency of zigzag and open rings and about 50% pollen abortion, was reported by Levan (1939) in *Allium cernuum.* However, in *A. ammophilum* with a low frequency of terminalization, segregation was adjacent, seldom zigzag.

In interpreting the effect of terminalization on chromosome segregation, Gairdner and Darlington (1939) suggested that the ring with non-terminal chiasmata was more compact and rigid than when the chiasmata were only terminal. In 1937 Darlington and Gairdner stated that the absence of terminalization prevents regular zigzag orientation of the chromosomes in a multiple ring. Gairdner and Darlington (1931) suggested that the different segregations are the result of two assumed forces: (a) repulsion

between the two poles and the associated chromosomes, (b) repulsion between the paired chromosomes, probably localized at the centromeres. The latter was supposed to act more strongly along the axis of the spindle to repel adjacent chromosomes in the ring and to orient them on opposite sides of the equator. Then a gradual movement onto the plate of the chromosomes along the ring would complete the alternate arrangement. Non-disjunction would be the result of different chromosomes in the ring establishing a relationship with the spindle independently. "Interstitial" chiasmata were believed to interfere with the gradual orientation along the ring. For example, in *Oenothera* it was suggested by Darlington (1937) and by Marquardt (1937) that when one chromosome establishes a relationship with the spindle, this determines the orientation of the other chromosomes in the ring. Ostergren (1950), in explaining the arrangement and behavior in *Oenothera* rings, stated that the chromosomes in the chain or ring dance around at prometaphase, a mutual pulling on one another resulting in orientation of adjacent chromosomes toward opposite poles. This works best when the chiasmata are terminal and the kinetochores are median. Kinetochores separated by the longer arms or by arms having a subterminal chiasma were supposed to be in effect too far apart for the mutual effect.

In species not showing mostly directed segregation, a higher proportion of the cells either shows no interaction between adjacent centromeres or else the chromosomes pass on to the metaphase plate simultaneously, adjacent chromosomes orienting more or less at random. Darlington (1937, p. 152–153) has stated that "an association with "interstitial" chiasmata is relatively rigid; its shape shows little variation, and is determined by the number and distribution of the chiasmata . . . . An association with terminal chiasmata is extremely pliable . . . . Forces of repulsion associated with the centromeres are therefore able to effect regular disjunction of a ring with terminal chiasmata although they are powerless to distort a configuration held together by numerous "interstitial" chiasmata". In 1939 he stated that "if chiasmata are terminalized a higher proportion of regular gametes are produced . . .".

H. Lewis (1951) has suggested that some factor associated with the sequence of the chromosomes in translocation multivalents,

not terminalization of chiasmata, may determine or insure alternate segregation. This is based on his observation that in *Clarkia elegans* the rings normally show alternate segregation, but that in ring-bearing plants with extra chromosomes adjacent as well as alternate segregations were observed in the configurations having one or more extra chromosomes. In these same plants some of the configurations with only four chromosomes also showed adjacent segregation. These were assumed to be cases in which one of the four was one of the extra chromosomes.

A few other possible exceptions may be mentioned, although the information on them is incomplete. In *Nicotiana,* Mallah (1943) reported that in polar view, most of the cells showed the translocation ring flat on the metaphase equatorial plate, supposedly in a position from which alternate or adjacent segregation of the chromosomes could occur. In 1952 he reported that in the analyzable figures the chromosomes were zigzag in arrangement. At metaphase I *Nicotiana* chromosomes are very short.

For *Hypericum punctatum,* Hoar (1931) stated that the metaphase I chromosomes tended to show alternate segregation, yet about half the pollen was aborted at maturity. (There may have been other causes of abortion. Also the extent of alternate segregation was not stated).

One extreme is Haga's report (1943) of almost complete pollen abortion and no seed set in *Lilium hansonii* with a ring of four + 10 II. His explanation was that orientation of the ring was almost always such as to result in adjacent segregation. Thompson and Hutcheson (1942) in discussing translocations in wheat, regarded the segregation as basically alternate, but thought that special conditions interfered and gave the appearance of randomness. They concluded that the forces which cause chromosome segregation involve whole chromosomes.

The above evidence has been mainly from cytological observations. In a few species there is other evidence on meiotic behavior of the chromosomes in rings. In maize, by using interchanges involving chromosome 6 which has the nucleolus organizer as a marker, the frequencies of the different kinds of chromosome segregations have been determined (McClintock, 1934, and unpublished; Burnham, 1949, 1950b). When one break is in the arm which has the nucleolus-organizer, and there is no

crossing-over in the interstitial segment, both alternate and adjacent-2 segregations produce spore quartets in which each of the four spores has one organizer and therefore one nucleolus. Those from adjacent-2 segregation all abort but those from alternate are all normal. Adjacent-1 segregation brings about non-disjunction for the organizer region, and in the resulting spore quartet two spores have no organizer (diffuse or scattered nucleoli); the other two have two organizers (potentially two nucleoli). Crossing-over in the interstitial segments (between the breaks and the centromeres) followed by alternate or adjacent-1 segregation results in a distinctive type of spore quartet having only one spore with diffuse nucleoli.

By combining counts on frequencies of spore quartet types with counts on pollen abortion, the frequency of crossing-over and the kinds of segregation were determined [15]. When both interstitial segments were short, alternate segregation was roughly 50%, the remainder being made up of adjacent-1 and adjacent-2 segregations in about equal proportions. When at least one interstitial segment was very long, there was little or no adjacent-2 segregation. These relations were observed in one experiment in which the interstitial segment was greatly shortened by the introduction of a homozygous pericentric inversion. This shifted the centromere of one chromosome much closer to the interchange point while retaining the same arm lengths of the cross-shaped interchange configuration.

In one group of ring-forming interchanges with short interstitial segments there was an average of about 25% of adjacent-2 segregation. Therefore the length of the interstitial segment is one factor affecting the segregation (Burnham, 1949, 1950b). Relative length of the two axes does not seem to be a factor. In most of the translocations used for those studies, the pachytene length of the axis with the centromeres was equal to or much greater than that of the other axis. In two [16] of them, however, the centromere-bearing axis was much shorter than the other, a ratio

[15] The kinds of spore quartets expected after the various possible crossovers have been calculated and diagrammed independently by Khan (1947, 1954). The frequencies expected with different degrees of interference were calculated by him on the assumption that there is a ratio of 2 alternate : 1 adjacent 1 : 1 adjacent 2 segregations regardless of break positions. The experimental data on maize do not support this assumption.

[16] Subsequent information indicated that in the third one, supposed to be of this type, the axes were nearly equal in length.

of about 1 : 2, respectively; yet adjacent-2 segregation was 25.4% in one and 36.0% in the other. Hence the relative lengths of the two axes do not seem to be a factor determining the type of segregation.

In translocation heterozygotes which always formed chain configurations, there was very little adjacent-2 segregation, regardless of whether the interstitial segments were long or short. This accounts for the excess of adjacent 1 over adjacent 2 segregation (31 : 19 per cent) observed in the T5-6c heterozygote homozygous for the pericentric inversion in 5. At diakinesis, 46% of the configurations were chains. Other experiments show that both alternate and adjacent-1 segregations occur following crossing-over in the interstitial segment, possibly with equal frequency (Burnham, 1953). The pollen abortion was close to 50 per cent, regardless of whether the interstitial segment was long or short (Burnham, 1949, 1950b). Therefore in maize, when there is a ring configuration and interstitial crossing-over has not occurred, it is as if the ring may orient as an open configuration in two ways, giving rise to adjacent-1 or to adjacent-2 segregations; and that for each there is a corresponding zigzag or alternate configuration (all of one type), resulting in 50% of alternate segregations. When there is crossing-over in an interstitial segment, the chromosomes that cross-over pass to opposite poles, but both alternate and adjacent-1 segregations occur with relatively high, if not equal, frequencies (Burnham, 1953). In such figures, if the centromeres may pass to either pole independently, the two types of segregation would be in 1 : 1 ratio.

Adjacent-2 segregation occurs only in the ring configurations in which no interstitial crossing-over has occurred. This describes the behavior in maize but does not explain the mechanism. If, as Darlington says, the configurations with interstitial cross-overs are rigid, it is difficult to explain why they have enough flexibility to produce alternate as well as adjacent segregations in maize. Also, the configurations without such cross-overs should be free to react to the centromere effect which, according to Darlington, should bring about alternate segregation. In maize interchanges with short interstitial segments, this would be a large proportion of the meiocytes, yet alternate and adjacent segregations are about equally frequent.

The frequencies of the different kinds of diakinesis configura-

tions, and probably the segregation, may be affected by what appear to be rather small differences in chromosome morphology. Two examples may be cited: a) McClintock (1934) found that T6-9a normally showed a ratio of about 1 ring : 1 chain configuration, but when a chromosome 6 with a modified satellite was present, there was a low percentage of rings. b) In the studies of segregation in the two T5-6c heterozygotes, the one homozygous for the pericentric inversion in chromosome 5 had a much higher frequency of chain configurations (Burnham, 1950; Kahn, 1955). In this stock the centromere was much closer to the center of the "cross".

In a translocation in *Sorghum versicolor,* which involved the chromosome with the nucleolus-organizer, Garber (1948) found only two types of quartets, the cross-over type being absent. From quartet and pollen abortion counts he concluded that alternate segregation was about 50% with 23.2% of one type of open ring and 26.8% of the other.

Studies of chromosome segregation in translocations in the ascomycete *Neurospora crassa* have been reported by McClintock (1945) and by Singleton (1948). The segregation was not directed but appeared to be more like that in maize.

In *Drosophila* information on the segregation types and frequencies has been obtained from crosses between individuals heterozygous for the same translocation, and with genetic markers which permitted recognition of individuals coming from the union of gametes carrying complementary deficiencies and duplications; as well as those from normal gametes (Dobzhansky, 1930a). The relations between segregation and crossing-over in interstitial segments were approximately the same as in maize except that alternate segregation was considerably higher than 50% in certain translocations (Dobzhansky and Sturtevant, 1931; Glass, 1935)[17]. Novitski (1951) reported evidence from inversions in *Drosophila* that when crossing-over produces pairs of chromatids that differ considerably in length, the second division segregation is not at

[17] This inequality may not be real, but due in part at least to characteristics of those experiments: *a*) since there is no crossing-over in the ♂, the proportions of the segregation types should not be the same in both sexes; *b*) crossing-over in interstitial segments results in types which would be scored as alternate and as adjacent-1 segregations in a 1:1 ratio; *c*) Non-random second division segregation of the chromatid pairs following crossing-over in the interstitial segments.

random. When meiosis results in a linear quartet of cells, the longer chromatids are oriented more frequently so they will pass to the two middle cells, the shorter ones to the terminal cells. The frequency of this type of orientation was about .7 in place of the .5 expected if at random. It was pointed out that translocations in which the exchanged pieces differ greatly in length would, as a result of crossing-over in the interstitial segment, produce chromatid pairs of unequal length which should show non-random segregation at division II. Novitski showed that this could explain the approximate 2 : 1 ratio of complementary non-disjunctional offspring (from adjacent segregations) obtained by Glass (1933, 1935) for three different translocations in *Drosophila*. Zimmering (1953), in a study of one of the translocations used by Glass, confirmed the relationship between non-random disjunction and the production of chromatid pairs of unequal length by crossing-over. In maize translocations, such non-random orientation should have no effect on the degree of ovule or pollen abortion. If it occurs as described, it should result in an inequality of the complementary cross-overs in the interstitial segment.

Another possibility is that the difference between species showing directed segregation and those not showing it is determined genetically, as suggested by Frolik (1948) and others. Tests have been made in our own laboratory to locate exotic strains of maize which might have genetic factors determining directed segregation, but the results thus far have been negative. The method used has been to cross the exotic strains with an interchange having short interstitial segments, then backcross once to the exotic and observe the ratio of normals : semisteriles in the progeny. These tests are valid only for major genes. If multiple factors are involved, more backcrosses are needed. Dobzhansky (1951, p. 127) stated that Rhoades has unpublished evidence in maize for genetic control of segregation. This evidence, according to a personal communication from Rhoades is the following: By using genetic markers, a chain configuration of three chromosomes was shown to have mostly alternate segregation in certain plants, and approximately random segregation in certain sibs. This has not been observed in rings of four.

Garber (1950, 1954a, b) has suggested that if directed segregation is genetically determined, the two types of diploid ring-form-

ing species, one showing directed, the other non-directed segregation, should show the same differences in segregation in experimentally produced autotetraploids. He has observed that the multivalents in one tetraploid species of sorghum are zigzag and open in about equal frequencies, while in two others the multivalents are mostly zigzag.

One bit of evidence against genetic factors affecting segregation in rings is an observation by H. Lewis (1951) for *Clarkia elegans*. In that species the rings show regular alternate segregation, yet in a tetraploid sector the quadrivalents showed both alternate and adjacent segregations. Also in barley, in which the translocations show low sterility and supposedly directed segregation, Tsuchiya (1953) reported alternate and open configurations approaching a 1 : 1 ratio in the tetraploid.

Selection for low sterility within a heterozygous translocation line appears to be a promising approach to determining whether segregation is affected by genetic factors (Ramage, unpublished).

In conclusion, it appears that directed segregation in certain species may be accompanied by certain cytological features, but that these features may not be present in other species showing directed segregation. Further studies are needed to establish the facts in a larger number of species.

BEHAVIOR IN POLYPLOIDS

In polyploids the presence of multipartite configurations may be a consequence of the polyploidy, the multivalents being made up either of completely homologous chromosomes or of only partially homologous chromosomes (termed by Huskins "homoeologous"). The presence of chromosomes of unequal length in the multivalent configurations at meiosis may be an indication that translocation has occurred; e.g., in *Zebrina pendula* ($2n = 24$) two $\odot 4$ were observed, but they contained unequal chromosomes (Darlington, 1929a).

Stebbins, Valencia and Valencia (1946) have stated criteria which may distinguish between higher chromosome associations that are true multivalents as a result of polyploidy from those due to structural hybridity. Those arising because of the latter are always simple rings or chains, the chiasma frequency in the bivalents being different from that in the higher associations, the

frequency in the latter different from that in polyploids. Also in many cases the number of chromosomes associated in one group is too high not to be attributable, in part at least, to structural heterozygosity.

In *Bromus* hybrids the association of unequal chromosomes in pairs at meiosis has been reported by Walters (1954) to be due to a stickiness of the matrix. The resulting "pseudo-bivalents" are not an indication of earlier chromosome change.

Another type of behavior is that in which there are configurations with a higher number of chromosomes than expected from the probable degree of polyploidy; e.g., *Rosa relicta,* 2n = 28, supposedly a tetraploid, was reported to have some associations of four, five, six or eight chromosomes (Erlanson, 1931). Also *Aucuba japonica* (2n = 32) had associations of four, six or eight chromosomes (Meurman, 1929a, 1930). No attempt has been made to include all which may be of this type. A few are included in the survey by families which follows. See also Stebbins (1950).

Autotetraploids from diploids which had translocations have been studied also. The gigas form of *Oenothera lamarkiana* described by de Vries was an autotetraploid. Linnert (1948) reported studies of tetraploid *Oenothera,* but these were produced from races with seven chromosome pairs. An autotetraploid line of *Rhoeo discolor* has been reported by Walters and Gerstel (1948). The kinds and frequencies of the various configurations were about as expected from the known homologies in the diploid. There was no increase in frequency of pairs in spite of the fact that each chromosome in the autotetraploid had an exact duplicate available. Another example of an autotetraploid carrying a known translocation is in *Datura stramonium* (Bergner, 1944). For further details on the behavior of the latter two, see pages 494 and 485 respectively.

In the allopolyploids the deficiency-duplications which arise from the translocation heterozygotes may be viable, e.g., in *Gossypium hirsutum* and in *Triticum.*

VALUE AND USES OF INTERCHANGES

Anderson (1935) has summed up the uses of interchanges in his general statement that they are of special value in building up a knowledge "of such items as the location of given genes on the

observed chromosome thread, and the linkage relationships of conspicuous markers on the chromosomes; also to make available means of marking or of controlling desired portions of chromosomes". Also see Muller (1954, pp. 439–462). Examples of specific and general uses are:

1. They have demonstrated the relations between chromosomes and genes, between chromosomes and linkage maps. Prediction of genetic results made from cytological observations, and vice versa, have been in agreement.
2. They have furnished information on chromosome behavior which resulted in marked advances in cytology. Among the special cytological problems for which interchanges have been or may be used as tools, the following may be listed:
   a. Proof that when genetic crossing-over occurs, a cytological cross-over also has taken place: maize (Creighton and McClintock, 1931; Brink and Cooper, 1935); *Drosophila* (Stern, 1931).
   b. Evidence that broken ends become attached only at broken ends. Interchanges have been found that were so unequal that only in very favorable cases could they be shown to be reciprocal, e.g., where the short piece is recognizable cytologically: *Drosophila,* maize.
   c. Factors affecting chromosome segregation: maize, *Drosophila, Oenothera.*
   d. The nucleolus and its relation to one chromosomal element, the organizer region; maize (McClintock, 1934).
   e. Pairing of chromosomes at meiosis, the points at which it is initiated, and its variation to include non-homologous pairing and the effect on recombination in maize (McClintock, 1932, 1933; Burnham, 1932b, 1934b).
   f. Chiasma position, also chromosome contraction, in relation to regions differing in density of staining: tomato (S. Brown, 1949; Barton, 1951).
   g. Comparison of break frequencies in different regions of the chromosomes.
   h. The kinds of segregation which occur after crossing-over in interstitial segments: maize (Burnham, 1953).
   i. The relation between genetic cross-over length and

physical length along the chromosomes: *Drosophila* (Dobzhansky, 1930b, 1932b; maize (Anderson and Brink, 1940; Anderson et al., 1955a, b).

j. The effects of changed chromosome morphology on cytological behavior, e.g., extremely short vs. long chromosomes.

k. The influence of the centromere or of heterochromatin on crossing-over by shifting segments from their normal positions: *Drosophila* (Beadle, 1932b; Mather, 1939).

l. Studies on the effect of temperature and other conditions on the association of chromosomes in rings: *Oenothera* (Oehlkers, 1936; Zürn, 1937, 1941); *Rhoeo* (Straub, 1936).

m. Preferential segregation and the formation of supernumerary spindle fibers at meiosis: referred to by Rhoades (1952) in maize.

n. The use of unequal translocations to demonstrate that crossing-over has preceded chiasma formation (Parthasarathy, 1940). These demonstrate also that the first division is reductional at the centromere (Burnham, 1932a). They may be used to study chiasma frequencies in different regions in the translocated chromosomes (Menzel, 1955).

3. They have been used to identify the linkage group carried by each chromosome, e.g., in maize, barley and *T. monococcum;* in determining the orientation of the linkage group in the chromosome (maize), the position of genes in the physical chromosome (maize, *Drosophila*), and the locus of the centromeres in the genetic linkage groups (maize, barley).

For the latter, homozygous interchanges may furnish critical information if they are used to determine which genes in the two linkage groups are still linked and which are not, as illustrated by Anderson and Randolph (1945) in maize. If a linkage is found which did not exist in normal stocks, one of the genes is in a translocated segment, the other in the segment which carries the centromere. If the orientation of the linkage group is known for one of the two chromosomes interchanged, and if certain of the gene markers used for that chromosome are known to be in one arm, others in the other

arm, then the centromere-bearing portion may be distinguished from the translocated segment.

If there is directed segregation, the expected reduction in crossing-over in the interstitial segments may give a clue to the positions of the centromeres. For example, Hanson (1952), for three interchanges with breaks at different positions in one linkage group, presented data which showed reduction in crossing-over for regions marked by three genetic factors. The observed shift in the region of greatest reduction was taken as an indication of the probable position of the centromere. Lamm (1949a) suggested similar use of such data in *Pisum*. This is true if the reduction in crossing-over is due to the relation between type of disjunction and recovery of cross-overs and therefore is confined to the interstitial segment. In a species such as maize, in which the reduction appears to be due mainly to the effect on pairing in regions adjacent to the break, the reduction is not confined to the interstitial segment but is greatest in the regions closest to the break. Some reduction may occur at times even in the non-translocated arm, since the abnormal pairing has been observed cytologically to extend across the centromere in certain translocations, not in others (Burnham, unpublished).

The waxy gene, which gives a red-brown color test in endosperm and pollen with iodine solution, was used by Patterson (1952) to determine whether, in translocations involving chromosome 9, the break in 9 was between the *wx* locus and the centromere or in the other arm. For this test only interchanges which involved chromosome 9 and had one of the interchanged pieces short enough so that the pollen deficient for it was partially filled, could be used. In the interchange heterozygote, it was necessary to have the *wx* allele on the normal chromosome and *Wx* on the interchanged chromosome. Then if the break were in the arm not carrying that locus, the partially filled grains were mostly *wx;* if the break were between it and the centromere, they were mostly *Wx*. These relations are seen if diagrams are drawn.

4. Interchanges may be useful in establishing the independence of linkage groups identified previously only by genetic means (Kramer, Veyl and Hanson, 1954; Burnham, 1955 in ms.).

5. They may be used to compare the effects of contrasting parental chromosomes or chromosome combinations: maize (Anderson, 1935, 1952).
6. Those with sufficiently long interstitial segments are useful in testing for the presence of megaspore competition, by comparison of pollen with ovule abortion. If there is competition, the ovule abortion will be less. This test in maize gives no evidence of competition (Burnham et al., 1954).
7. They are useful in locating new genes and in studying the inheritance of complex characters; e.g., they have been used to study smut resistance, oil content of the kernel, corn borer resistance, *Helminthosporium* resistance, and pericarp tenderness in maize (see p. 513 for references).
8. They may be used to link a character recognizable as an endosperm or seedling character with one recognizable only at a later stage, for chemical or physiological studies of the contrasting types at the earlier stages in segregating populations: (Anderson, 1952; Teas et al., 1952).
9. They may be useful in transferring a chromosome with a desired character into an inbred, suggested in maize (Anderson, 1943).
10. In derivatives from species crosses, in which the desired character is carried by an extra chromosome, a translocation may transfer the segment with the desired gene to the normal set of chromosomes. An example in which this was brought about by using X-rays is in *Godetia* (Hiorth, 1942b, 1947c; Håkansson, 1943). In a *Vicia* species cross, an intermediate type arose in F_2 as the result of a translocation (Sveshnikova, 1932). Sears (1951, 1955) has achieved the transfer of leaf rust resistance from *Aegilops* to *vulgare* wheat by X-rays, probably as the result of an insertional translocation.
11. They may be used to produce internal duplications for known regions of chromosomes. This has been accomplished in *Drosophila, Datura,* and probably in maize. (For *Drosophila,* Muller, 1956 and earlier; for *Datura,* Blakeslee et al., 1936; and for maize, Gopinath and Burnham, 1956.) By adding gene material in which new mutations might occur, they may be important in evolution.
12. A ring which links all the chromosomes has been suggested

as a means of producing inbred lines in maize or new varieties in barley (Burnham, 1946).

13. Such a big ring with balanced lethals might be of practical value in some crops, since it might be essentially true breeding for at least part of the heterosis it might show.

    In crosses between *Oenothera* races, in which all or most of the 14 chromosomes are in a large ring at meiosis, segregation is limited to a few types, frequently only two, which differ greatly in many characters but which show no intergradations. A cross involving many of the same characters but in which the chromosomes in F_1 were present either as 7 II or as a ⊙4 plus 5 II was reported by Emerson (1928a). For most of the characters there was a wide range of segregation typical of quantitative inheritance. Even with multiple factor inheritance, the big ring in *Oenothera* effectively limits the segregation.

14. They might be used to build up stocks which, although normal in fertility themselves, would give very high sterility in crosses. This might be desirable in certain horticultural crops, e.g., in melons.
15. The translocation heterozygotes are useful as sources of trisomics, both tertiary and primary. These in turn are useful in locating genes in the chromosomes: maize, barley.
16. If the translocation is very unequal, a duplication plus deficiency type may survive and be useful in linkage tests: maize (Patterson, 1952); *T. monococcum* (L. Smith, 1948). In an allotetraploid with such a translocation it is possible to determine which of the various deficiency-duplications are viable (Menzel, 1955).
17. McClintock (1945) has shown their usefulness in Ascomycetes in studying chromosome segregation, also in determining the frequency with which aberrant alignments of the eight spores occur because of irregularities in spindle orientation or because of transposition of spores.
18. Translocations have been used in two *Sciara* species to aid in a study of the unusual chromosome behavior in connection with the inheritance and determination of sex (Crouse, 1943).
19. Translocations have been used to determine whether a given pair of chromosomes is the sex-determining pair: Chinese hamster (Yerganian, 1953).

20. They have been used to study the behavior of supernumerary or "B" type chromosomes in maize, using interchanges between them and the primary chromosomes (Roman, 1947).
21. In silkworms, translocations in which an X-chromosome carrying a dominant color gene (in one stock for egg color, in another for larval color) was transferred to the W chromosome, provided easy recognition of the sexes in the early stages. This could be very useful for commercial purposes. It also offers the possibility of utilizing the males for silk production, since the male gives fibers of better quality and higher yield (work of Tazima, summarized by Kihara, 1953).
22. An interchange between a "B" chromosome and a primary one has been used to distinguish between the role of the endosperm and that of the embryo in determining the expression of a character in maize, i.e., vivipary of the embryo appeared whenever the embryo was homozygous recessive (Robertson, 1952).
23. In allopolyploids, translocation heterozygotes may be used as sources of monosomics, e.g., in cotton (Menzel and Brown, 1952) and *Nicotiana* (Mallah, 1952). The former suggested that the duplication + deficiency types which are viable may serve to locate genes in specific portions of the chromosomes.
24. An unequal translocation has been used to determine the genome affinities in crosses with diploid species (Menzel, 1955).

INTERCHANGES IN INDIVIDUAL SPECIES

Brief summaries are given in the following for each species. They are arranged alphabetically by family, and the genera under each are in most cases in alphabetic order. The Gramineae are divided into two groups: Cereals and "Other Grasses". For convenience in locating a species, an alphabetical list of the genera follows, together with the family to which each belongs.

ALPHABETIC LIST OF GENERA

Angiosperms

A. DICOTYLEDONEAE

Aconitum—Ranunculaceae
Antirrhinum—Scrophulariaceae
Arachis—Leguminosae
Aucuba—Cornaceae
Beta—Chenopodiaceae
Brassica—Cruciferae
Campanula—Campanulaceae
Campsis—Bignoniaceae

Chelidonium—Papaveraceae
Clarkia—Onagraceae
Crepidiastrum—Compositae
Crepis—Compositae
Datura—Solanaceae
Eucharidium—Onagraceae
Fragaria—Rosaceae
Gaillardia—Compositae
Galeopsis—Labiatae
Gaura—Onagraceae
Gilia—Polemoniaceae
Glycine—Leguminosae
Godetia—Onagraceae
Gossypium—Malvaceae
Helianthus—Compositae
Humulus—Cannabinaceae (Moraceae)
Hypericum—Hypericaceae (Guttiferae)
Luffa—Cucurbitaceae
Lycopersicum—Solanaceae
Matthiola—Cruciferae
Nicotiana—Solanaceae
Notonia—Compositae
Oenothera—Onagraceae
Paeonia—Ranunculaceae
Paraixeris (see *Crepidiastrum*)—Compositae
Petunia—Solanaceae
Phlox—Polemoniaceae
Physalis—Solanaceae
Pisum—Leguminosae
Plantago—Plantaginaceae
Polemonium—Polemoniaceae
Primula—Primulaceae
Raphanus—Cruciferae
Rhododendron—Ericaceae
Rosa—Rosaceae
Rumex—Polygonaceae
Salix—Salicaceae
Solanum—Solanaceae
Stizolobium (*Mucuna*)—Leguminosae
Vicia—Leguminosae
Viola—Violaceae

B. MONOCOTYLEDONEAE

Aegilops (see *Triticum*)—Gramineae (cereals)
Agrostis—Gramineae (other grasses)
Allium—Liliaceae
Aloe—Liliaceae
Alopecurus—Gramineae (other grasses)
Anthoxanthum—Gramineae (other grasses)
Avena—Gramineae (cereals)
Brachypodium—Gramineae (other grasses)
Briza—Gramineae (other grasses)
Brodiaea—Liliaceae
Campelia—Commelinaceae
Carex—Cyperaceae
Crocus—Iridaceae
Dactylis—Gramineae (other grasses)
Eleusine—Gramineae (other grasses)
Elymus—Gramineae (other grasses)
Festuca—Gramineae (other grasses)
Fritillaria—Liliaceae
Gasteria—Liliaceae
Hordeum—Gramineae (cereals)
Lilium—Liliaceae

Miersia—Amaryllidaceae (Liliaceae)
Musa—Musaceae
Najas—Naiadaceae
Nerine—Amaryllidaceae
Nothoscordum—Liliaceae
Oryza—Gramineae (cereals)
Pancratium—Amaryllidaceae
Paris—Liliaceae
Pennisetum—Gramineae (other grasses)
Polygonatum—Liliaceae
Puccinellia—Gramineae (other grasses)
Rhoeo—Commelinaceae
Scilla—Liliaceae
Secale—Gramineae (cereals)
Setcreasea—Commelinaceae
Sorghum—Gramineae (cereals)
Strelitzia—Strelitziaceae (Musaceae)
Tradescantia—Commelinaceae
Tripogandra—Commelinaceae
Trillium—Liliaceae
Triticum—Gramineae (cereals)
Tulipa—Liliaceae
Vallisneria—Hydrocharitaceae
Zea—Gramineae (cereals)
Zebrina—Commelinaceae
Zephyranthes—Amaryllidaceae

Gymnosperms

Cephalotaxus—Taxaceae
Taxus—Taxaceae

Fungi

Aspergillus—Ascomycetes
Neurospora—Ascomycetes
Saccharomyces—Ascomycetes

ANGIOSPERMS

DICOTYLEDONEAE

Bignoniaceae—bignonia family.

Campsis. *Campsis Tagliabuana* is a natural hybrid of *C. chinensis* and *C. radicans.* The F_1 has 50% sterility, but has 20 pairs and regular pairing (Sax, 1933). Sax suggested segmental interchange in one or both parental species as the explanation.

Campanulaceae—campanula family.

Campanula. In *Campanula persicifolia,* which " exists in numerous geographic races in different parts of Europe and in a variety of diploid and polyploid forms in cultivation ", ring formation was first reported by Gairdner and Darlington (1930, 1931). Straub (1936) found that at high and low temperatures there were more interstitial chiasmata than at normal temperatures. Part of the plants used had a ⊙4. Straub (1938) and Wiebalck (1940) used these same lines in further studies on meiosis. No comparisons appear to have been made of the behavior of the bivalents as compared with the chromosomes in the ring.

In collections of the diploid forms of *Campanula persicifolia* (n = 8) from 16 localities in Europe, five had plants with a ⊙4 (Darlington and Gairdner, 1937; Darlington and La Cour, 1950). Darlington (1939) referred to Gairdner's unpublished observation of a ⊙4 in a diploid. Of five cultivated forms, one had plants with a ⊙4. One diploid line derived from a tetraploid had a ⊙6 (Darlington and Gairdner, 1937). Both the natural and the cultivated forms were stated to be low in fertility. The plants with a ⊙4 were intercrossed to produce plants with 2⊙4 or a ⊙6. These were crossed with the ⊙6 derived from the tetraploid. Plants with the largest rings were selected for further crosses. After four generations, plants with a ⊙10 or with a ⊙12 were obtained (Darlington and Gairdner, 1937). Test crosses of the rings of various sizes showed that the larger ones failed to give plants with anything but smaller rings. No cross-overs which might have combined the different translocations were recovered. Selfs of the plants with rings of various sizes, ⊙6, ⊙8, ⊙10, ⊙12, gave no normal offspring with eight chromosome pairs (35 offspring tested), but crosses between sisters or non-sisters did (Darlington and La Cour, 1950). When the wild forms with a ⊙4 were selfed, they also gave no 8 II offspring. These results were interpreted as indicating a chromosome and gene balance which favored hybrids heterozygous for less favorable factors.

In two cases a ring of eight broke down into two interdependent rings of four. That is, the chromosomes in the two rings could form only two kinds of functional gametes instead of the four expected if the rings were independent. (See page 437).

The metaphase associations of four chromosomes observed in a triploid and of five, six, seven or eight chromosomes in the tetraploids are evidence of the presence of chromosomal interchanges (Gairdner and Darlington, 1931).

According to Darlington et al., this species is like *Datura* and *Oenothera* in usually having complete terminalization of the chromosomes. No information was given on the orientation of the chromosomes in rings at meiosis, due to difficulties of observation.

Cannabinaceae—hemp family.

Humulus. Kihara (1929) reported that in the pollen mother cells of certain plants of *Humulus japonicus* (2n = 17), a short

pair of autosomes (SS) was united with the three sex chromosomes at diakinesis. There were 6 II plus the pentapartite configuration in the order Y S S X Y. At times the configuration was separated into smaller groups.

In *H. lupulus,* Sinoto (1929) reported 8 II plus a ring of four chromosomes in the ♂. Alternate chromosomes were said to pass to opposite poles[18]. Also two of the chromosomes differed from each other and were smaller than the other two. He suggested that this might be a sex chromosome complex.

Chenopodiaceae—goosefoot family.

Beta. Levan (1942) observed two heteromorphic bivalents in one diploid (2n = 18) plant from a cross between a triploid and a diploid sugar beet, *B. vulgaris.* Evidence that an interchange had occurred was the fact that sometimes these were associated in a chain of four, or a chain of three + I. Pollen fertility was 82%.

Compositae—composite family.

Crepidiastrum, Paraixeris. In a naturally occurring hybrid between *Crepidiastrum Keisukiana* (n = 5) × *Paraixeris denticulata* (n = 5), cells with two associations of four chromosomes plus one II were the most frequent (Ono, 1948). There was 24.6% of good pollen.

Crepis. Navaschin (1926) grew and checked cytologically, 4,000 plants of *Crepis tectorum* (n = 4) and 2,000 of *C. capillaris* (n = 3). In the former, 43 plants had a recognizable chromosomal change. Most had a change in chromosome number; but a few had changes in the chromosomes, including a difference in trabant size, and one with a large V-shaped chromosome. In 1931 he attributed the latter to translocation.

Levitsky and Araratian (1931), Levitsky, Shepeleva and Titova (1934), Levitsky and Sizova (1934), Petrov (1935), Korjukaev (1940) reported translocations produced by X-rays in *Crepis capillaris* (n = 3). Most and perhaps all of the translocations were reciprocal (Levitsky and Sizova, 1935). In a more detailed study of the root-tip chromosomes of the progeny of plants X-rayed as seedlings, Levitsky (1940) listed the numbers with translocations between the different chromosomes. Certain ones were between members of the same pair, from which a balanced combination could not be obtained. He established homozygous stocks of

[18] The intention may have been to state that they went to the same pole.

different translocations, and intercrossed them. The pollen fertility of two heterozygotes (⊙4) was 47%. He reported trisomics in the progeny of the heterozygotes. For two translocations established by Levitsky, Arenkova (1939) determined the kinds of spores and their frequencies based on first divisions of the microspores. In both translocations the frequencies of the two spore types, resulting supposedly from alternate segregation, deviated greatly from the expected 1 : 1 segregation. Also only one of the two possible types of adjacent segregation was observed. Certain of the n + 1 types were observed also. One difficulty with this method of determination is that the different kinds of spores may not develop at the same rates (McClintock, 1938) and hence a sample at any one time may not have the various types in their true proportions. Levitsky (1940) reported that spores resulting from adjacent segregation were functional in some cases, that aberrants with duplications were found in the progeny of one of the translocations, but not in the others. A line descended from X-ray treatment produced chromosomal aberrations at a much higher rate than normal, part of these being typical translocations (Levitsky, 1937).

Petrov (1935) stated that in a D-C and a D-A translocation, the new D chromosome was only about one-third its normal length. Chain configurations were the rule, but in 72 and 90% of the cells, respectively, the new D was not paired, resulting in a high frequency of n + 1 spores. It was noted also that in about 30% of the cases the chromatids of one chromosome at the end of the first meiotic division were unequal, evidence that crossing-over takes place between two of the four chromatids of a chromosome pair.

Kostoff (1949) reported translocations produced by neutron treatment of dry seeds of *C. capillaris*, and established the homozygote for one of them.

Gerassimova (1935) found two translocations in the progeny of old seeds of *Crepis tectorum* (n = 4). In 1939 she reported two translocations produced by X-raying pollen of *C. tectorum* (n = 4); one between the B and C chromosomes, the other between A and D (D is the satellited pair and is attached to the nucleolus). In the heterozygous condition each produced a chain of four chromosomes. The A-D translocation, when heterozygous, produced

slightly more than 30% seed set. Homozygous types were established which were fertile and normal in appearance. When the two were crossed, the F_1 had two chains of four and 30% fertility. In 1940 Gerassimova reported a B-D translocation in which the break in D was in the satellite, and that in B was near the centromere, the new "satellite" thus being a long piece of B. The heterozygote had 30.1% sterility. "Cripples" and "dwarfs" appeared in the progeny of this translocation heterozygote due to partial or complete loss of the part of "B" transferred to the "D" chromosome, this loss occurring at the somatic divisions (1940b). The satellite thread often was long and stretched with the "satellite" off the metaphase plate. At times the thread was broken and the satellite not included in the nucleus, or a bridge was formed and the satellite broken and reduced in size. Tertiary trisomics were observed in the progeny of the various translocations, from which she established the four primary trisomics.

Avery (1930) discussed translocations as one means of changing chromosome morphology and number in *Crepis*.

Tobgy (1943) found in the hybrid between *Crepis neglecta* (2n = 8) and *C. fuliginosa* (2n = 6) an association of four and of three chromosomes as well as various other configurations. He concluded from the morphologies and the pairing that unequal reciprocal translocations could be the explanation. A transfer of the essential genes to another chromosome by unequal translocation followed by a loss of the one chromosome remnant no longer essential was suggested to account for the decrease in chromosome number.

Sherman (1946) observed one or two associations of three chromosomes and of five in some cases in the progeny of crosses between *C. kotschyana* (n = 4) and other species with n = 5. The E chromosome of the 5 II species was associated with the C^k–C^x chromosomes in the F_1 (C^k = the C chromosome from the 4 II, C^x from the 5 II species). Unequal translocations were assumed to have occurred. Six translocations were shown to have occurred in *C. kotschyana* or its ancestor, several small ones in the 5 II species.

Gaillardia. In hybrids between different wild races of *Gaillardia pulchella,* Stoutamire (1955) observed 15 II + ⊙4, 13 II + 2⊙4 and 11 II + 3⊙4. More complex associations were found in the

same plants indicating other structural differences. One hybrid with a ⊙4 had 95% stainable pollen, another had only 26%. Since doubling the chromosome number reduced the sterility, the conclusion was that the sterility was due to structural differences rather than to incompatible gene combinations.

Helianthus. The F_1 hybrid *Helianthus tuberosus* (n = 51) × *H. annuus* (n = 17) had 32 to 34 bivalents (Kostoff, 1939c). The occasional multivalents were interpreted as resulting from small structural differences, including translocations.

Notonia. Ganesan (1939) reported a cross-shaped configuration at pachytene in one of two wild plants of *Notonia grandiflora* (2n = 20). It formed mostly a ⊙4 at diakinesis, but about 23% of the cells had a chain at metaphase I. The chiasmata in the ring were terminal in all but one of the cells observed, yet only 48% of the configurations were disjunctional. About 2% of the pollen was aborted, but 73% of the ovules did not develop seeds. The heterobrachial condition of the chromosomes (centromeres not median) was suggested as the cause of the high frequency of non-disjunctional separation in spite of the terminal position of the chiasmata. Based on the cytological observations on disjunction, pollen abortion should have been higher. Polyploidy might explain this.

Cornaceae—dogwood family.

Aucuba. In *Aucuba chinensis* (2n = 16), Kihara and Yamamoto (1935) found a tetrapartite ring, the result of segmental interchange. It was usually a zigzag at metaphase and fertility was high.

In *Aucuba japonica* (2n = 32), an autotetraploid, Meurman (1929a, 1930) reported rings or chains of six and eight chromosomes in addition to the quadrivalents expected from tetraploidy, a result explainable by the presence of segmental interchange.

Cruciferae—mustard family.

Brassica. In *Brassica juncea* (2n = 36), *B. monensis* (2n = 24) and *B. nigra* (2n = 16) Sikka (1940b) observed an occasional association of four chromosomes. In *B. wrightii* (2n = 24), associations of four up to ten chromosomes were found. At least the higher ones were due probably in part to translocation.

In an F_1 hybrid between two species which showed only ten bivalents, *B. tournefortii* and *B. trilocularis,* there were many univalents, a few bivalents, and in about a third of the cells an association of three or of four chromosomes. The latter was taken to indicate an interchange as one of the differences between the two.

In *B. oleracea* (2n = 18), Richharia (1937) reported a ⊙4 or a chain in every cell of the two plants examined.

Raphanus. In two horticultural varieties of *Raphanus sativus* (2n = 18) Maeda and Sasaki (1934) observed an association of four or six chromosomes at diakinesis of meiosis. The configurations were seen only rarely at metaphase. Fukushima (1937) reported two translocations among various types of sterility in *R. sativus* due to chromosome aberrations. In 1949 he described two new lines with translocations. These were diploid (2n = 18) descendants of a hybrid between the *Raphanobrassica* amphidiploid and a tetraploid radish. One line had 80% pollen sterility, and 2⊙4 + 5 II, the other had 50% pollen sterility and a ⊙4 + 7 II.

Cucurbitaceae—gourd family.

Luffa. In the interspecific F_1 hybrid *L. cylindrica* × *L. acutangula,* Pathak and Singh (1949) observed an association of four chromosomes in about a third of the cells, plus mostly pairs but some univalents. They concluded that during differentiation of the two species a structural change had occurred in the chromosomes. Both parents had 13 II.

Matthiola. In two strains of *Matthiola incana* (2n = 14) Philp and Huskins (1931) observed occasional associations of chromosomes, two cases (cells) with six chromosomes, four cases with four chromosomes either in a string or a ring. The low frequency of these associations was interpreted as indicating the pieces exchanged were short. A triple chiasma in one cell was taken to indicate reduplication of a segment. They suggested that the duplication-deficiency combinations from interchange may have functioned.

Ericaceae—heath family.

Rhododendron. In one clone of *Rhododendron,* Belling (1925) reported that two pollen grains in each tetrad were empty. This may have been the result of translocation, inversion, or of a deficiency.

Hypericaceae—St. Johns-wort family.

Hypericum. In *Hypericum punctatum* (2n = 16) a distinct species growing throughout New England and farther south and west, the 16 chromosomes were always either in a ring or in a chain, observations being based on megasporogenesis as well as microsporogenesis (Hoar, 1931). The metaphase I chromosomes tended to separate so that alternate chromosomes passed to the same pole. About half the pollen was aborted. Sixteen other species of *Hypericum* were examined, but all showed nothing but pairs of chromosomes (Hoar and Haertl, 1932).

Labiatae—mint family.

Galeopsis. In *Galeopsis speciosa* (2n = 16), plants with 40 to 50% sterility segregated normal and partly sterile plants in a 1 : 1 ratio. The partially sterile plants continued to segregate and the normals bred true, a breeding behavior typical of that of semisterility (Muntzing, 1938). Two fertile and three partially sterile plants were examined cytologically. One of the latter showed a 4-chromosome association in over 50% of the cells; the other two did not.

In *Galeopsis tetrahit* (2n = 32), an allotetraploid, some 30 lines were tested in intercrosses, not in all combinations. Certain crosses gave partial sterility in F_1, some roughly 25% pollen abortion, others roughly 35 to 45%. Ovule sterility was present also. Partially sterile plants always gave segregating progenies, and normals bred true (Müntzing, 1929, 1930). Crosses between certain lines gave independent segregation for two genetic characters, but in another cross the two were linked (Müntzing, 1930, 1932). In the latter the F_1 was 45% sterile. These results all suggest chromosomal interchange. In an attempt to determine whether structural change could explain the breeding results, I have summarized his data on 24 of the intercrosses in which certain lines were used in several crosses, and assumed that when the F_1 was partially sterile, one of the lines was homozygous for an interchange; if normal in F_1, that both lines were the same, either normal or homozygous interchange. Nineteen of the crosses fit, the other five do not.

Müntzing (1938) reported that two lines, J and X, which were fertile inter se, gave the same results in F_1 when crossed with nine

other lines. Other lines showed various degrees of similarity. In his earlier studies there was normal cytological behavior, whether the plant was partially sterile or normal. The F_1 plants from certain of his crosses had an occasional association of three chromosomes plus a univalent. In the B × C cross which showed the typical semisterility type of inheritance (and which also had shown the linkage of two factors which normally were independent), as mentioned earlier, no three- or four-chromosome associations could be found. He stated that certain of the later generation progenies of B × C showed much later flowering, as if a duplication-deficiency gamete may have functioned. He concluded that pollen sterility and disturbed chromosome pairing are different symptoms of structural differences between the lines crossed; and that the sterility in the *Tetrahit* F_1's is due entirely or mainly to such structural differences.

Crosses between *G. Tetrahit* and *G. bifida* gave partially sterile F_1's, but in F_2 there was a normal curve of variation for sterility—not a two-peaked curve as in the intra-specific crosses (Müntzing, 1929).

Leguminosae—pulse family.

Arachis. In the peanut, *Arachis hypogea* (2n = 40, probably polyploid), associations of three, four, five, six and ten chromosomes were observed by Husted (1936).

Glycine. In the soybean, *Glycine hispida* (2n = 38), Williams and Williams (1938) reported breeding results from a cross which indicated that a line descended from X-rayed material was homozygous for a translocation. Heterozygous plants had about 50% of shriveled pollen and about 44% undeveloped ovules in the pods which matured. Correction for loss of pods with no viable ovules raised the per cent of undeveloped ovules to 50.8%. One of the eight genes segregating in the cross showed linkage with the translocation (14% recombination).

Williams (1948) reported that most, but not all, of the plants of the wild soybean, *Glycine ussuriensis,* appear to have a chromosomal arrangement different from the domestic type, the F_1 having approximately 50% of aborted pollen and ovules.

Pisum. In *Pisum sativum* (2n = 14) the first translocation was discovered when close linkage of two normally independent charac-

ters was found in certain crosses (Hammarlund, 1923, 1927–8). Cytological examination showed the plants had 5 II + ⊙4 and that they were partially sterile (Håkansson, 1929, 1931; Hammarlund and Håkansson, 1930). At least 13 different naturally occurring translocations have been reported in *Pisum* and the chromosomes identified on the basis of intercross results (Håkansson, 1929, 1932; Richardson, 1929; Sansome, 1931, 1932, 1933, 1937, 1938a, 1939, 1950; Lamm, 1951; Nilsson, 1933, 1936, 1950). Each of the seven chromosomes is involved in at least one translocation. Some were found as occasional partially sterile plants, others were located by the sterility in F_1 of crosses between lines. At least four cases of partial sterility were recognized by Lamprecht (1939, 1944, 1946, 1948, 1951a, 1953, 1954) in crosses between different lines.

Sterility in the translocation heterozygotes with a ⊙4 appears to be about 50 per cent; and in those that have been studied, the proportion of zigzag to other arrangements at meiosis I was about 1 : 1. From one ⊙6 type resulting from a cross between two translocations, Sansome (1938a) established in homozygous condition the cross-over which combined both translocations. She also reported a ⊙4 in a cross between two translocations which involved the same two chromosomes, but with breaks probably at different points.

Recurrence of the same translocation supposedly has been observed in certain varieties, the suggested explanation being that crossing-over had taken place between duplicated homologous short segments in otherwise non-homologous chromosomes (Lamprecht, 1939, 1952; Lamm, 1947)[19]. Ten cases have been described in which a character is determined by two polymeric genes (genes with similar phenotypic effect), the F_2 ratios being 15 : 1 or 9 : 7 (Lamprecht, 1953a). He considers these as evidence that such duplicated segments in non-homologous chromosomes exist. He reported also (1939, 1949) that the frequency of translocation when non-parchmented lines mutated to parchmented was much higher than in other normal material. These translocations have been established (Lamprecht, 1954).

[19] One supposed case was in the Extra Rapid variety. Sansome (1950) showed that the original translocation in that variety involved chromosomes 3 and 5, while the Swedish line involved 2 and 3 (based on the linkages reported by others).

Lamprecht (1954) has summarized the genetic data on the various cases of partial sterility in his crosses and certain of those previously reported. Caroli and Blixt (1953) have made a cytological identification of the chromosomes involved in one of these translocations, one for which the two linkage groups had been determined by Lamprecht (1953).

A similar correlation of genetic and cytological studies has been made for line 21 (Lamprecht, 1955a; Blixt, 1955). One line contained a translocation but gave fertile hybrids when crossed with normals. This was interpreted as indicating a simple translocation combined with a duplication which masked the sterility which otherwise would be expected (Lamprecht, 1955b). Caroli and Blixt (1955) found changes in the lengths of two different chromosomes in root tip divisions.

A translocation complex was observed in the F_1 of crosses between other species, e.g., *P. humile* × *P. arvense* (Håkansson, 1936a); also in *P. abyssinicum* × *P. sativum* (G. von Rosen, 1944). Sansome (1938b) observed one association of four chromosomes in most of the cells and occasionally a second one in a cross of *P. humile* with *P. sativum*. The pairing relations and the effect of certain derivative lines on genetic ratios indicated more than one structural difference. There was no translocation in the line of *P. humile* used by Lamprecht (1951b) in the cross with a translocation race of *P. sativum*. Sutton (1935) also referred to a cross of *P. sativum* × *P. humile* which gave a complicated double translocation configuration.

Sansome and Sansome (1940) reported completely sterile plants segregating in the progeny of a translocation heterozygote and suggested they might be due to deficiency or duplication associated with the translocation. Lamprecht (1954) reported that sterile dwarfs segregated in the F_2 of two crosses with one line but not in other crosses with that line, the suggested explanation being that the dwarfs were the result of a deficiency.

A dominant gene (Q) for ovule abortion was reported by Wellensiek (1928) and Wellensiek and Keijser (1929). Lamprecht (1945) mentioned the possibility that it might have been a case of structural hybridity.

Trisomics have been observed among the offspring from plants heterozygous for a translocation (Sansome, 1933; Nilsson, 1936;

Håkansson, 1936b; Sutton, 1939). Sutton listed the various types of trisomics expected and considered the theoretical genetic ratios.

Linkages have been reported for several of the translocations in *P. sativum* (Hammarlund and Håkansson, 1930; Nilsson, 1933, 1950; Pellew, 1931, 1937, 1940; Lamm, 1948, 1949b, 1950, 1951; Lamprecht, 1939, 1946, 1953c, 1955a, b). Lamprecht (1953b) reported data showing reduced recombination due to interchange.

Four of the known linkage groups are identified with the corresponding chromosomes (Blixt, 1955).

Stizolobium (*Mucuna*). Belling (1914a, b, 1915a) found semisterility in F_1 of crosses between *Stizolobium deeringianum* and other species of velvet beans, and the typical breeding behavior. This was explained later (1924) on the basis of a chromosomal interchange between non-homologues. The segmental interchange hypothesis for *Stizolobium* was based solely on genetic evidence (Belling, 1928). After describing the tertiary trisomic mutants in *Datura,* Belling (1927) stated that in all crosses with the one species of *Stizolobium,* occasional plants (about one in 200) appeared which were peculiarly leaved, small and nearly sterile. He suggested that these were probably tertiary mutants which arose following 3–1 disjunction in the ring. See pages 421 and 429 for a lengthier description of the breeding behavior.

Vicia. Savchenko (1935) reported the production of chromosomal translocations in *Vicia sativa* (vetch) by X-rays and that certain progeny were homozygous for the change.

Hybrids between *Vicia sativa* (n = 6) and *V. amphicarpa* (n = 5) showed an association of three chromosomes in F_1 (Sveshnikova, 1932; Sveshnikova and Belekhova, 1935). This association was made up of the large A and the F chromosomes of *sativa* paired with the A of *amphicarpa.* Among the F_2 plants there was one with two changed chromosomes, a 2-armed A and a shorter F-chromosome, supposedly the result of an unequal reciprocal exchange. In F_2 there were often two types of plants, one like *V. amphicarpa* with ten chromosomes, the other mutational and always heterozygous for new translocation chromosomes. The latter never produced the homozygous translocation in six generations from the mutants. A new intermediate line originated in F_2 as the result of translocation. She concluded that inter-specific hybridization could be a source of new chromosomes as new morphological units in evolution.

The cross *V. sativa* × *V. angustifolia dolichosomica* showed open rings of four chromosomes (Sveshnikova, 1936).

Malvaceae—mallow family.

Gossypium. Gerstel (1953) reported observations on crosses between several strains of different species of diploid Asiatic *Gossypiums* with 2n = 26. *G. arboreum,* when crossed with *G. herbaceum* or with *G. anomalum,* produced F_1 plants with a $\odot 4 + 11$ pairs. Therefore *G. arboreum* differs from the other two species by one translocation. In the first hybrid, seed abortion varied from 4.4 to 16.5%; pollen abortion from 43.3 to 45.0%. The cross of *G. anomalum* with *G. herbaceum* had 13 II.

Iyengar (1945) reported an association of four chromosomes in many or most of the 52-chromosome plants extracted from different interspecific crosses between the allotetraploid American (2n = 52) and the diploid Asiatic (2n = 26) species backcrossed to the American. The association was believed to be due partly to structural differences, including translocation.

In hybrids between the American upland cotton, *G. hirsutum* (2n = 52), and *G. arboreum,* Gerstel (1953) found two associations of four and six chromosomes most frequently, indicating they differed by three translocations. *G. hirsutum* × *G. herbaceum* showed $2\odot 4$ and therefore differed by two translocations.

Brown and Menzel (1950) reported frequent multivalents in three-species hybrids. Menzel and Brown (1954), in a reexamination of certain of the three-species and other polyploid hybrids, have shown that translocations present in certain subgenomes will explain the observed multivalents. An excess of multivalents observed in the three-species hybrids is accounted for by pairing between chromosomes belonging to different subgenomes. They discuss the translocations in relation to the transfer of desirable genes from other species to the cultivated cottons.

Translocations in *G. hirsutum* produced by atomic bomb irradiations have been reported by Brown (1950). One of these usually formed a chain (Menzel and Brown, 1952) and had a chiasma in the interstitial segment in most of the cells. From these cells an equal proportion of disjunctional and non-disjunctional gametes is expected. Several of the latter functioned to produce plants deficient for either a translocated or a non-translocated segment. A simple monosomic type was found in the

progeny of one of these. An induced translocation in *G. hirsutum*, in which the pieces exchanged were very unequal, was used to demonstrate that a " wide array of viable, fertile deficiency-duplication genotypes was recovered from the translocation heterozygote " (Menzel and Brown, 1952; Menzel, 1955). This translocation served to determine the genome affinities of the two translocated chromosomes in crosses with diploid species (Menzel, 1955).

Onagraceae—evening primrose family.

Translocations have been reported in the following genera: *Clarkia, Godetia, Eucharidium, Gaura* and *Oenothera*. In the treatment by Lewis and Lewis (1955), the species described as belonging to the genus *Godetia* are considered as species of *Clarkia*. Likewise *Eucharidium concinnum* is designated *C. concinna*.

Clarkia (*Godetia*). Lewis and Lewis (1955) list 33 annual species of *Clarkia* of which 32 occur in western North America, one in South America. Of the 29 diploid species and subspecies listed in their table 1, 11 had some plants with at least one configuration of four or more chromosomes. One of the polyploid species, *C. purpurea* (n = 26), had one or more multiple chromosomes associations in interpopulation hybrids (p. 304). Håkansson (1931a) reported that two out of three plants of *Clarkia elegans* (*C. unguiculata* according to Lewis and Lewis) had a ⊙4 plus 7 II, the ring being oriented usually as a zigzag configuration. H. Lewis (1950, 1951, 1953a, 1954) reported that in part of its range in western North America, a large proportion of the individuals had supernumerary chromosomes and that many plants from such populations had a ring or a chain of four, two associations of four or an association of six chromosomes. All showed regular alternate separation of the chromosomes with normal fertility. The plants with supernumeraries were not phenotypically different from the others, but the extra chromosomes were believed to have arisen from the translocation rings by non-disjunction (Lewis 1954). Although no morphological change could be detected, Lewis (1954) stated that there is some evidence of a shift in the adaptive potentials in these plants. Håkansson (1925) observed a chain of chromosomes in *Godetia amoena* (*C. rubicunda*).

Hiorth (1941, 1942a, 1947b) reported the breeding behavior,

and Håkansson (1940b, 1941a, b, 1942, 1943a, 1944b, 1947) the cytology of several garden races and wild populations of *Godetia* species and a number of hybrids. Certain garden races of *G. whitneyi* (*C. amoena*) were mixtures of plants with 7 II, ⊙4 or ⊙6 (Hiorth, 1942a; Håkansson, 1942). In two races with a ⊙6, none of the progeny had 7 II. In one of these, many of the families segregated lethal chlorophyll deficient plants. These did not show the common degeneration with inbreeding, suggesting that they were true-breeding heterozygotes. The plants with rings showed only 2 to 5% of poor pollen.

The wild races of *G. whitneyi* displayed a much greater variation in morphology and chromosome structure (Hiorth, 1942a; Håkansson, 1942, 1947). Crosses between certain races of *G. whitneyi,* which had only paired chromosomes, were structurally heterozygous in F_1 (unpublished results of Mooring, cited by Lewis, 1953). Håkansson (1941a) first reported a wild race of *G. whitneyi* with a ⊙12 + one II. In northern Oregon four out of nine collections had a ⊙4 plus a chain of 3 + 1 or a ring or chain alone, the other collections had 7 II. In the Redwood Highway race (farther south) different plants had 7 II, ⊙4, ⊙6, ⊙6 + ⊙4, ⊙8, 2⊙4, ⊙10, or a ⊙12. In the various plants with a large ring, one complex seemed to be the same, and this same complex was present also in most garden races. This differs from the usual situation in *Oenothera,* in which each of the two complexes in a race carries different translocations, and the complexes differ in different races.

Hiorth (1948a, b, c) reported that in crosses between certain wild races of *G. whitneyi,* 50 or 100% of the F_1 seedlings were lethal. The explanation arrived at was that each of the two parents in such a cross was heterozygous or homozygous for an independent dominant factor which was complementary to the one carried by the other parent for a lethal effect in F_1. The double heterozygote was usually lethal. Håkansson (1942) considered the large ring race of *G. whitneyi* as an unfinished true-breeding heterozygote of the *Oenothera* type and suggested the following as possible reasons for its failure to be completed:

a). The chromosomes are larger than in *Oenothera,* possibly making it more difficult to form a constant ring.

b). Inversions and duplications were believed to be present in certain of the rings.

c). One pair of chromosomes had subterminal centromeres. Since these chromosomes were never seen in a ring, it was believed that such centromeres frequently cause deviations in the zigzag arrangement.

d). In certain races, interstitial chiasmata in the bivalents were frequent. These were believed to cause deviations in the zigzag arrangement.

The following were reported also by Håkansson (1941a): a ring of four chromosomes in *G. bottae—typica* (*C. bottae*) (n = 9); a chain of three unequal chromosomes + I in *G. parviflora* (*C. speciosa*) (n = 9), and one or two groups of four, or a group of six + a group of four in *G. tenella* (*C. tenella*) × a garden form.

Hybrids between two colonies of *C. biloba,* subspecies *brandegeae* had a large translocation (Roberts and Lewis, 1955). Hybrids between *C. biloba* (n = 8) and *C. lingulata* (n = 9) usually had a ⊙4 and a chain of five (Roberts and Lewis, 1955; Lewis and Roberts, 1955).

Pseudomonosomic races were reported also in certain collections of the wild *G. whitneyi* races (Håkansson, 1942, 1943b, 1944a, 1945b, 1946; Hiorth, 1947a, 1948a, b, d) these having 4 II + a chain of 4 + I = 13 chromosomes. It was believed that the decrease in number was the result of translocations which transferred the essential gene-carrying segments of one chromosome to other chromosomes. The nullisomic (2n = 12) was not viable in progeny from selfing, but some were obtained in the progeny of race crosses.

A tertiary trisomic was reported by Håkansson (1940a) in *G. whitneyi,* and by Lewis (1954) in *C. unguiculata.*

Eucharidium. In *Eucharidium concinnum* (*C. concinna,* according to Lewis and Lewis) (n = 7), Schwemmle (1926) figured a chain of six chromosomes at diakinesis, but most cells showed a ⊙4.

Gaura. In another related genus, *Gaura,* with about 20 species in Mexico and temperate North America, Bhaduri (1941, 1942b) has reported studies of two garden species. In *G. lindheimeri* he found a ⊙6 + 4 II in certain plants, 2⊙4 + 3 II in others. In *G.*

biennis the maximum catenation he observed was a ⊙12 + one II, but he referred to an unpublished report by Burkert of a ⊙14. He stated that alternate segregation in the rings was the regular thing, but that irregular types were fairly frequent. Both *G. biennis* and *G. lindheimeri* bred true when selfed. He suggested, based on comparisons of chromosome morphology, that *Gaura* and *Oenothera* may have had a common ancestor.

Oenothera. The extensive cytogenetic work on the many races belonging to the subgenus *Euoenothera* of the genus *Oenothera* will be reviewed only in a general way here.

The reader is referred to reviews by Cleland (1936), Sturtevant (1926, Renner's studies on *Oenothera* genetics), Darlington (1929b, 1931a, 1939), Emerson (1935), Renner (1946) and Stebbins (1950), and to a series of papers by Cleland (1950a, 1950b), Cleland and Hammond (1950), Cleland, Preer and Geckler (1950), Geckler (1950), Hagen (1950), Hecht (1950), Preer (1950) and Stinson and Steiner (1955). Translocations in *Drosophila* and their bearing on *Oenothera* problems have been discussed by Sturtevant and Dobzhansky (1930, 1931), Muller (1930), and by Dobzhansky and Sturtevant (1931).

This subgenus comprises many species and races. The North American races do not cross readily with the South American ones, but inter-crosses within each group are easily made. The North American races have been tentatively placed in eight groups, based on their range of distribution and cytological features; a *hookeri* group in western U.S. has 7 II or only small rings; a small *irrigua* group in New Mexico has rings including only part of the chromosomes. The other six groups are characterized by complete rings of 14 chromosomes and are found in different sections of the U.S., including the Rocky Mountains, plains, mid-western, eastern, northeastern and southeastern States (Cleland, 1940; Cleland, Preer and Geckler, 1950).

The South American races also range from 7 II to complete rings of 14 chromosomes (Hagen, 1950). In both groups of races, those with large rings are nearly true-breeding. The North American ones with large rings have small or intermediate-sized flowers and are self-pollinated, those with small rings or all pairs have large flowers and are open-pollinated. The true-breeding characteristic is the result of the presence of balanced lethals which

may be zygotic or gametic or various combinations of both. Even the segregation for quantitative characters is limited when a large ring is present (Emerson, 1928a). At meiosis, in the majority of the cells, alternate chromosomes pass to the same pole [20]. This has been based on cytological observations of the naturally occurring rings at metaphase. Since the chromosomes have a definite order in the ring and are associated because of interchanges of end segments of non-homologues, this results mainly in only two types of gametes, the two parental combinations of chromosomes. It results also in a linkage of the characters which come from each parent. Each gametic combination is referred to as a "complex" and has been given a distinctive name; e.g., the two complexes formed by *Oe. lamarckiana* are *gaudens* and *velans* which differ from each other and from the complexes in other races by having different chromosome ends interchanged in part of the chromosomes. The heterozygotes are more vigorous than homozygous races, hence here is a mechanism to perpetuate heterosis in a nearly true-breeding form.

The interchanges which have survived in the evolution of Euoenothera races are those in which the pieces exchanged are of about the same length, as indicated by the fact that the chromosomes of different races have median centromeres and show little difference in size. There seems to be very little crossing-over in the interstitial segments (between the centromere and the point of exchange)[21]. The differential segments (between the different breaks in the same chromosome) in general are short also, if present at all, although there is evidence that there are differential segments in certain races. Emerson (1936) has discussed the evidence on this latter point. He used the term "interstitial", however, to refer to the segments now referred to as "differential". Interchanges with long interstitial segments would be

[20] The alternate segregation of the chromosomes appears to be brought about by the method of orientation following diakinesis. At that stage, open rings are observed. After this, it is as though one chromosome were to pass on the metaphase plate in advance of the others; then as the next adjacent ones come on the plate, they orient toward the opposite pole, successive ones being oriented in relation to these. For suggestions as to why this occurs, see pp. 444–452. It seems to be characteristic only of certain species.

[21] Marquardt (1918) has pointed out that the heterochromatin proximal to the centromeres may be a factor in decreasing crossing-over if the breaks are farther away from the centromere. Also crossing-over is localized in the distal portions.

expected to show sterility as a result of the crossing-over in those segments. Hence there seems to have been a natural selection against these. This is supported also by the fact that these types, which are missing in the natural populations, have been produced in *Oe. blandina* (7 II) by X-rays (Catcheside, 1954; Marquardt, 1948). In the report by Catcheside (1954) the segregations in these rings were also mostly alternate, with a few adjacent-1, and they also showed partial sterility. Sikka (1940) suggested that the origin of a 7 II mutant from a line with $2\odot 4 + 3$ II might have been the result of a new segmental interchange.

Several of the other subgenera belonging to the genus *Oenothera* also show ring configurations, certain of which include all the chromosomes, are true breeding complex heterozygotes, and also show a preponderance of alternate segregation of the chromosomes (Cleland et al., 1950; Haustein, 1952). Other races show smaller rings. Races belonging to the subgenera *Anogra, Hartmannia, Lavauxia, Raimannia* and *Salpingia* have been found with rings.

Papaveraceae—poppy family.

Chelidonium. In *Chelidonium majus* ($2n = 14$), Nagao and Saki (1939) observed a closed ring of ten chromosomes. Four of the chromosomes had a median centromere, six had a terminal one. The arrangement on the meiotic metaphase plate was usually zigzag. They observed 68.97% of empty pollen and 71.88% of empty seeds.

Plantaginaceae—plantain family.

Plantago. In *Plantago contorta,* a line of *P. major,* Ikeno (1923, 1925) observed a plant with a mean of 55.1% empty seeds. Its breeding behavior was explained on a two-factor hypothesis similar to the one originally used by Belling to explain the inheritance of semisterility. This suggests that an interchange or an inversion may have been present. *Plantago Rugellii* is listed as having 4 II + 4 IV to 8 II + 2 IV (Heiser 1953).

Polemoniaceae—phlox family.

Gilia. An occasional association of three or of four chromosomes in a chain, indicative of translocation, was observed by Grant (1954) in hybrids produced by crossing certain leafy-stemmed

species (n = 9), i.e., *Gilia anglensis* × *G. millefoliata* and *G. millefoliata* × *G. capitata.* Similar configurations were more frequent in crosses made between woodland species, i.e., 2.3% in *G. caruifolia* × *G. splendens* and 22.9% in *G. australis* × *G. splendens* (Grant and Grant, 1954).

Phlox. Meyer (1940) stated that certain collections of *P. paniculata* had an association of four chromosomes + 5 II at metaphase I of meiosis.

Polemonium. In *Polemonium coeruleum* (2n = 18) J. Clausen (1931a) reported a white-flowered type had 7 II plus an association of four chromosomes and suggested the interchange explanation. Two races of *P. reptans,* when crossed, produced two plants, one of which showed an association of three or of four chromosomes, usually only one in each cell. These configurations were usually zigzag chains.

In the published figures, the hybrid of *P. mexicanum* × *P. pauciflorum* had an open chain of six chromosomes or an open chain of three plus a ⊙3; *P. filicinum* × *P. coeruleum* had two open chains of three. These were interpreted as the result of interchange (Clausen, 1931a).

Polygonaceae—buckwheat family.

Rumex. In *Rumex angiocarpus* (2n = 14) a hybrid between two karyotypes showed an association of four chromosomes in addition to four pairs + XY, or an association of three and a univalent and 5 II, or 7 II (A. Love, 1944). Most of the configurations had the zigzag orientation.

In *Rumex acetosa* (2n ♀ = 14, 2n ♂ = 15) Kihara and Yamamoto (1931) found a plant with an unexpected V- and a J-shaped chromosome in somatic plates. In a male from one cross involving that plant, a chain of four chromosomes or of three plus a univalent was observed in addition to the 3-partite sex chromosomes ($X + Y_1 + Y_2$) (Yamamoto, 1933, 1935b). The pollen was about 50% visibly aborted. The configuration was interpreted as the result of simple translocation. He reported finding in the progeny plants which came from non-disjunction in the chain, and suggested that this is a possible explanation for the existence of various karyotypes in that species (Yamamoto, 1937a, b, 1938). He also

cautioned against concluding that a giant V-shaped chromosome is an X- or a Y-chromosome.

A cross between *Rumex acetosa* and *R. montanus* had 50% decrease in fertility but there was no configuration at meiosis to indicate interchange (Yamamoto, 1935a).

Quadrivalents and associations of higher numbers of chromosomes have been reported in two polyploid species: *Rumex tenuifolius* (2n = 28) (Löve, 1944) and *R. acetosella* (2n = 42 or 41) Löve, 1944; Kihara, 1925, 1927).

Primulaceae—primrose family

Primula. In *Primula pulverulenta* (n = 11) with long- and short-styled forms, Wanner (1941) reported one plant which at meiosis showed chains of three, four, five and six chromosomes, the sequence of chromosomes in the chain being constant. The evidence is in favor of interchange. On small numbers, disjunctional and non-disjunctional configurations were about equally frequent. Pollen observations were not reported, but it had only about 50% of the normal number of seeds. In a monomorphic species, *P. cockburniana* (n = 11), there were no such configurations. The cross between the two species also showed a ring or a chain of four chromosomes (Wanner, 1941).

Brunn (1930) reported that the members of a pair of homologues differed from each other in length or in other morphology in *Primula fauriei, P. fasciculata* and *P. szechuanica,* probably the result of translocation.

Ranunculaceae—crowfoot family.

Aconitum. Afify (1933) reported that in each of three diploid species of *Aconitum* (n = 8) from Helltal, Austria—*A. orientale, A. luridum,* and *A. lycoctonum*—only 12 of the somatic chromosomes could be paired off, the other four not having mates. Shafer and La Cour (1934) mentioned that the somatic nuclei in some clones had morphologically odd chromosomes, indicating structural hybridity. Rings or chains were observed in 22, 16 and 11%, respectively, in the three species (Afify, 1936). Size distinctions were not large enough to determine the disjunction types from the rings. In the triploid species, *A. stoerkianum,* rings of four and chains of four, five, six or seven chromosomes were observed (21% of the figures). The associations in the four

species were interpreted as being due to segmental interchange. Leszczak (1950) reported that *A. variegatum* (2n = 16) was not carrying interchanges, since all the chromosomes could be paired off. As the genus moved from Asia westward, segmental interchange occurred in certain species.

Paeonia (2n = 10). One form of *Paeonia anomala,* an old world species, was heterozygous for an interchange of a large segment (Stebbins, 1938).

Two clones of *P. brownii* from the mountains of northern California and the Pacific Northwest had a complete ring of ten chromosomes, but the order of the chromosomes in the two clones was different (Stebbins and Ellerton, 1939). In *Paeonia californica,* which grows in colonies in the low hills of coastal southern California, the configurations at meiosis in different clones included 5 II, ⊙4, ⊙6, 2⊙4, ⊙8, ⊙6 + ⊙4 and a ⊙10. Also two structurally different but homozygous plants were collected (Stebbins and Ellerton, 1939; Walters 1941, 1942, 1953; Walters and Stebbins 1942). The latter paper reported the presence of numerous fragments also. Paracentric inversions were also frequent. The widespread occurrence of a structurally heterozygous bivalent (the mates differing in the centromere position) was reported (Walters, 1952). Inversion was suggested as the most probable explanation, although intra-chromosomal translocation was mentioned as a possibility. In some plants the heterozygous pair was in a ring of chromosomes.

In *P. anomala* most of the chiasmata were interstitial, while in the other species they were localized at the ends, the other portions not having been paired. The fertility of the form of *P. anomala* with the ⊙4 was much higher than that of *P. californica* with a ⊙6. In one multipartite ring of *P. californica* only 24% of the orientations were non-disjunctional. The higher sterility may have been due to causes other than the ring, but, being in a long-lived perennial, would have had little effect on survival.

In the diploid *P. smouthii* and the tetraploid *P. officinalis* (2n = 20), many of the chromosomes in the root tips did not have a morphologically similar partner (Dark, 1936). At metaphase of meiosis, members of bivalents were unequal. These were evidences that interchanges or other structural changes had occurred. In the diploid *P. delavayi,* an association of three or four chromosomes

was observed, but multiple chiasmata, in one case quadruple, indicated a reduplication of end segments.

Rosaceae—rose family.

Fragaria. A tetraploid which arose in F_1 of a cross between *Fragaria bracteata* and *F. vesca rosea* (in both species n = 7) was crossed with the parents and other 7 II species (Yarnell, 1929). In the resulting triploids (21 chromosomes) he observed usually ten disomes and an unpaired chromosome. He considered this as evidence of the complete pairing of non-homologues. One suggestion has been that the behavior may have been due to interchange, but more evidence is needed.

Rosa. In certain of the diploid roses (2n = 14), multipartite configurations which may have been the result of interchange have been reported (Erlanson, 1931, 1933), e.g., in *Rosa blanda* configurations with three, four or six chromosomes; and in a hybrid *Polyantha* (the Orleans variety = *R. multiflora*) complex configurations with four chromosomes. The pollen was 43% aborted in the former and 45% in the latter. She reported (1933) a ⊙4 in part of the cells in *R. woodsii* and in *R. pisiocarpa,* and " strings of chromosomes " in *R. salicetorum.*

There was a ring or a chain of four chromosomes in about 10% of the P.M.C. in a seedling from *Rosa hybrida,* variety Max Graf (Wulff, 1951). This seedling had double the number of chromosomes in the variety and was thought to be an amphidiploid (2n = 28).

The presence of one or more associations of four chromosomes in several tetraploid varieties (2n = 28), probably the result of interchanges, has been reported by Wylie (1954, pp. 57, 64).

Salicaceae—willow family.

Salix. Salix phylicifolia (n = 57) and the hybrid *S. nigricans* (n = 57) × *S. phylicifolia* form mostly bivalents, but there were some ring or chain configurations of three, four or six chromosomes (Håkansson, 1933). These were interpreted as the multivalents expected from polyploidy. In occasional trivalents in the hybrid one chromosome was larger than the other two, suggesting the presence of translocations also. These appear to be the examples in *Salix* of ring-formation due to translocation cited by Stebbins (1950).

Scrophulariaceae—figwort family.

Antirrhinum. In *Antirrhinum majus,* Ernst (1938, 1939) reported pachytene configurations indicative of translocations following heat or cold treatments, also as the result of X-rays. I have not seen any statement regarding translocations in the progeny. Pohlent (1942) found a few exceptional F_1 plants from a cross between two genetic stocks which were mosaic (variegated) for certain flower characters. Only the exceptional plants had a translocation complex at pachytene. One of the chromosomes involved was the same in the different mosaic plants. In one plant, at least four chromosome pairs were involved with foldbacks and other evidence of non-homologous pairing.

In a stock of *A. majus* mutable for one character, Mechelke and Stubbe (1954) reported that at pachytene there was a configuration of three chromosomes united at their terminal knobs. The union of two of them was believed to be the result of translocation involving not only heterochromatin but also a euchromatic region. The shift of heterochromatin to a position near the gene was proposed as an explanation of the mutability.

Solanaceae—nightshade family.

Datura. In *Datura stramonium,* the Jimson weed ($2n = 24$), Belling observed at meiosis in a trisomic type in Blakeslee's cultures a trivalent made up of one small chromosome attached to two large ones, and concluded that segmental interchange between non-homologues had occurred (Belling and Blakeslee, 1924). Blakeslee (1927c, 1928) reported that crosses between certain lines showed an association of four chromosomes which might or might not be associated with pollen abortion (also Bergner et al., 1933). They reported that those having mostly figure-of-eight configurations with an interstitial chiasma[22] were usually 50% sterile, while those mostly without these configurations had normal pollen or very low sterility. The ⊙4 or chain-of-four configurations were usually so oriented at metaphase I that disjunction was

[22] Interstitial chiasmata (between the translocation break and the centromere) followed by alternate segregation result in spore quartets in which two of the four spores are deficient and usually abort. They should account for most of the sterility in a species having mostly alternate segregation. That is, in *D. stramonium* since there is zigzag orientation, spore abortion should be low if most of the spore mother cells did not cross over in that segment; but would be about 50% if all had such cross-overs.

alternate. Blakeslee et al. (1937) stated that those which formed a ⊙4 had good pollen, those with mostly chains or frequent "pairs" had 25% up to 50% aborted pollen, while those with both interchanged pieces short, "necktie" configurations with two "pairs" associated at a common end—frequently not associated, had 50% abortion. Types which formed only chain configurations, never rings, were interpreted as being the result of simple translocations (Bergner et al., 1933; Blakeslee et al., 1933, 1937; Bergner and Blakeslee, 1934). These did not exist in nature, but only as a result of radiation. The evidence from maize suggests that most if not all are probably interchanges.

Blakeslee (1928) also reported that the cross of a primary trisomic with an interchange involving that chromosome broke the ⊙4 into a chain or string of five chromosomes. Tertiary trisomic types give similar configurations of five chromosomes. Their breeding behavior was summarized by Blakeslee and Avery (1938, p. 33); that of a compound chromosomal type by Blakeslee (1927a, b). Each of the primary trisomic types differed phenotypically from normals and from each other. The tertiary types showed part of the characters of each of the two corresponding primaries [23]. Another type has been termed a compensating trisomic (Blakeslee, 1931). The plants resemble a tertiary trisomic, but one missing chromosome of a bivalent is compensated for by its two portions being attached to segments of two other chromosomes. These latter two segments were present in addition to the normal number of pairs. Such a type might arise from certain 4-2 segregations in a ⊙6.

Satina et al. (1931) presented data from somatic mitoses on the cytological length and morphology of the extra chromosome in each of the primary trisomics and in the corresponding secondary trisomics. The same for the interchanged chromosomes in several of the interchanges was included.

To study the configurations in a tetraploid of known constitution for an interchange, Bergner (1944) produced a 4n line of

[23] Tertiaries $2n + 4.6$ occurred twice, $2n + 13.18$ twice and $2n + 2.9$ once, all spontaneously from the prime type I line (Blakeslee et al; 1937). They emphasized the fact that the complementary tertiary type was not found in the line. This may be a matter of chance tied up with the manner of nondisjunction as well as the time and method of origin, and the mode of detection.

prime type 1 and of prime type 2. In the cross of the two diploid lines, the usual translocation configuration at metaphase I was a ⊙4, although occasionally it was a chain or two "pairs". In the cross of the two tetraploid lines, the most frequent configuration had eight chromosomes; but in addition there were many others in which these eight were present as various types and combinations of associations of four, six or two chromosomes.

Tests for differences in chromosome organization in a large number of collections or from different geographical regions were reported by Blakeslee (1928), Blakeslee et al. (1937) and Bergner (1939, 1943). Plants from seed collections from widely different parts of the world were crossed with a standard line one and the F_1's examined cytologically. In these and a later report (Satina, 1953) a total of ten other types, five recurrent and five sporadic, had been found in 681 races (localities) tested. The standard line 1 (Prime type 1 or PT1) was the predominant type in the United States, Brazil and Japan; and it occurred also in several other countries. PT2 was the predominant one in Central America, Peru, Chile, Europe, Asia and Africa; others in other countries. Crosses between the "B" race PT2 and 14 other PT2's from various parts of the world all "formed equal bivalents" in F_1, the conclusion being that they were identical. They may not have been identical, since in maize "pairs" were observed also in the F_1's between interchanges involving the same two chromosomes but with breaks known to be at different positions (Gopinath, 1950).

Tests for differences in the chromosomes in different collections of other species have been reported also. In *Datura metel*, four types differing from a standard line were identified by Bergner (1943a). Results for other species of *Datura* were given by Bergner et al. (1941).

The chromosome organization of other species has been compared also with the standard line 1 of *D. stramonium* (Bergner and Blakeslee, 1932, 1935; Cummings, 1948; Satina, 1953). This has been summarized by Bergner (1943b) and by Satina (1953). *D. ferox* and *D. quercifolia* were crossed with each other and with *D. stramonium*, using an inbred line of each. The chromosome ends were identified in terms of the standard line 1 of *D. stramonium* chromosomes, by crossing with the tester prime types

of *D. stramonium*. For *D. ferox*, there were two types, each with seven new chromosomes; for *D. quercifolia*, three types, differing in six, seven and four chromosomes. They reported the result of intercrosses of *D. discolor* with the above species. An association of ten chromosomes was observed in the cross with *D. stramonium* (PT1). Crosses with certain of the prime types gave a configuration of 12, others gave a configuration of ten plus one of four. The chromosome ends of *D. pruinosa* were identified indirectly through crosses with another species, *D. leichhardtii* (Bergner and Blakeslee, 1943).

Cummings (1948) determined the end arrangements in *D. ceratocaula* and suggested a phylogenetic chart for the species.

The paper by Satina (1953) on *D. inoxia, D. meteloides* and *D. metel* completed the survey of chromosome end arrangements in the ten herbaceous species. Each of the 12 chromosomes of the standard line of *D. stramonium* has its ends rearranged at least once in the nine other species. She stated that there is no obvious direct correlation between the number of rearrangements and speciation or with incompatibility in crossing.

In *Datura* it appears that segmental interchange has accompanied speciation. In addition to the references given, the Annual Reports of the Genetics Department in the Carnegie Institution of Washington Year Books, Numbers 21 (1922) through 40 (1941), give other material on translocations in *Datura*.

Lycopersicum. In the tomato, *Lycopersicum esculentum* (2n = 24), an interchange ring-of-four chromosomes produced by X-rays was illustrated at diakinesis (S. Brown, 1949) and used in a study of chromosome contraction. It did not include the chromosome associated with the nucleolus. Barton (1951) reported that in another stock resulting from irradiation, most of the densely chromatic short arm of the chromosome attached to the nucleolus was involved in an interchange. At prometaphase all the associations of four chromosomes were chains resulting from a lack of chiasma formation in the short arm of the nucleolar chromosome. Of 140 analyzable figures, there were 88 chains, 46 pairs and six other configurations. No information was given on spore abortion or on breeding behavior.

Nicotiana. According to Goodspeed (1934), the formation of at least one association of three chromosomes in crosses between

Nicotiana tabacum (24 II) and the 12 II species—*tomentosa, sylvestris, tomentosiformis*—could be interpreted as evidence of reciprocal translocation within the *tabacum* complement. Also the observation that in *N. rustica* (24 II) × *N. undulata* (12 II) quadrivalents and sexavalents were frequent could be interpreted as the result of translocations within the *undulata* set. Goodspeed and Avery (1934) and Goodspeed (1936a, b) reported the production of translocations and other abnormalities as a result of X-ray treatment. Goodspeed (1937) mentioned that a series of homozygous losses had been established in the progeny of translocation heterozygotes in *N. tabacum*. He also stated that in the cross of *N. raimondii* × *N. solanifolia* at least six of the 12 II present were either heteromorphic or unequally aligned, indicating that translocations or inversions had occurred in their origin. Goodspeed and Avery (1939) reported tertiary trisomics in *Nicotiana sylvestris* (2n = 24), some in the progeny of plants with the asynaptic character, others from X-ray treatment; from which the presence of translocations may be inferred.

According to Kostoff (1941a), in haploids of *N. langsdorfii* (n = 9) about 4–5% of the cells had one or two usually dissimilar pairs. Pairs were observed also in haploids of *N. sylvestris* (n = 12), *N. rustica* (n = 24), *N. tabacum* and in certain amphidiploids. He reported that he had evidence of cross-over chromosomes and of mutant morphological types in the 2n offspring. No mention was made of chromosome associations in the offspring, but they might be expected. Kostoff observed occasional associations of four in a polyploid (allotriploid) from the amphidiploid *N. rustica* (2n = 48) × *N. paniculata* (2n = 24).

In *N. tabacum* the coral variant was shown by Clausen (1931) to be dependent on modification of the F chromosome. Later information indicated that coral was a translocation product, about half the cells at meiosis showing an association of four chromosomes plus 22 II (Lammerts, 1934, p. 39).

In hybrids between *N. tabacum* var. *Calycina* and other varieties, Kostoff (1943) reported associations of four chromosomes or of three plus a univalent, interpreted as indicating structural differences.

Goodspeed (1945, p. 544) referred to associations of three and higher numbers of chromosomes in interspecific hybrids (see his

summary for references). In 1947 he stated that races of at least one polymorphic species differed from one another by one to several reciprocal translocations.

Clausen and Cameron (1944) discussed the use of monosomics to identify the chromosomes in a translocation in allopolyploids. If the univalent chromosome were one of those involved, only three chromosomes would be associated in a chain in the monosomic plant.

Mallah (1943) saw ring configurations in intercrosses between non-commercial local South American varieties of *N. tabacum* (2n = 48) and a standard variety *purpurea*. Of 14 varieties tested, three gave a ⊙4, one gave a ⊙6 plus a ⊙4. These included none of the strictly commercial types. Intercrosses showed that eight chromosomes were involved in the translocations.

In 1952 he reported further studies of the ⊙4 in the hybrid which had a ⊙6 and a ⊙4. By selection in backcrosses to *purpurea*, the ⊙4 was retained. Pollen abortion was 11%, ovule abortion 16%, values which overlapped those of normal *purpurea*. The configuration was usually a ⊙4 with the chiasmata in the associated arms completely terminalized. In the figures that could be analyzed, the chromosomes were zigzag in arrangement. Normal plants and plants with a ⊙4 were about equally frequent in the progeny. As might be expected in an allopolyploid, deficient gametophytes resulting from adjacent segregation in the ring were occasionally viable. Only three of the four possible types expected from this kind of non-disjunction were observed. One of them was transmitted through both pollen and ovules, but more frequently through the ovules. In its progeny normal monosomic (2n − 1) types appeared in addition to monosomic types with one or both interchanged chromosomes. These were not observed in the progeny of the original ring. The chromosomes in the ⊙4 were identified by crossing with identified monosomics.

Cameron (1952) presented the results of testing 40 more varieties, a total of 55 in the two studies. The 26 large-seeded "more or less commercial types" had the same chromosome arrangement as *purpurea*. The 29 small-seeded varieties with weedier growth habit were homozygous for one or more translocations. The chromosomes of many were identified by use of

the monosomics and by intercrosses with one to four tester varieties. Nine varieties were of one type, 12 of another, and eight were different from these and from each other.

Müntzing (1935) observed frequent III and some fragments in the F_1 of *N. bonariensis* (n = 9) × *N. langsdorfii* (n = 9). The fragments, he suggested, might be due to crossing-over between transposed homologous segments, those having been the result of translocations.

Petunia. In *Petunia,* Welzel (1954) reported four reciprocal translocations produced by X-rays. Three had a ⊙4 and semi-sterility. The other was 67.8% sterile. The higher sterility was accounted for by irregular 3–1 segregation from the ring. According to the description, crossing-over in the short arm of the configuration fastened those two chromosomes together and resulted in the n + 1 and n − 1 spores. Both of these types were assumed to be inviable.

A race of *Petunia violaceae* (2n = 14) with an unstable mosaic flower color was examined cytologically by Telezynski (1935). In the eight plants, one member of one pair of chromosomes lacked the satellite. In some cells this chromosome was connected with another bivalent. Triple terminal chiasmata were observed, indicating a trisomic condition for one segment. The interpretation was that first an interchange of terminal segments of the two chromosomes had occurred, one of them being the end with the satellite. Subsequently the interchanged chromosome with the satellite was lost, and only one interchanged chromosome remained, the one without the satellite, the other bivalent consisting of two normal chromosomes. The chromosome change had nothing to do with the mosaic flower color. In this species the chromosomes were described as showing complete terminalization. The centromeres in the different chromosomes were not median but were at different positions.

Physalis (2n = 24). In a study of nine species of *Physalis,* seven species had normal pairing at meiosis; but two of them, *Ph. ankekengi* and *Ph. franchetii,* had a variable number of chains, univalents, open and closed bivalents at meiosis (Gottschalk, 1954). The number of chromosomes in the chains varied from three to eight. Pollen sterility was about 85%, and seed set per fruit was only about 25%. A basic configuration of ten associated chromosomes was proposed with a high failure of chiasma formation

which resulted in the chains, open bivalents and univalents. There were not enough analyzable figures to determine the relative frequencies of alternate and adjacent orientations of the chains.

Solanum. The literature on the cytology and genetics of *Solanum tuberosum,* the cultivated potato, and its relatives has been reviewed by Swaminathan and Howard (1953). In the diploids (2n = 24) an association of four chromosomes was frequently observed at meiosis in *S. verrucosum* with 61% sterile pollen; also a ⊙4, or at times III + I, or 2 II, or II + 2 I in *S. Rybinii* (Lamm, 1945). In *S. stenotomum* Lamm noted two pairs of unequal bivalents, one partner being similar to the T-chromosomes reported by Prakken and Müntzing (1933) in inbred rye. He suggested their origin through interchange, but there were no associations of four chromosomes. Müntzing (1933) observed multipartite associations in diploid and triploid *S. tuberosum.* In *S. tuberosum,* a tetraploid with 2n = 48 chromosomes, Stow (1926a, b) reported end-to-end union of nonhomologous chromosomes. An association of six was observed by Ellison (1936). Cadman (1943) observed associations of five and six. Meurman and Rancken (1932) reported hexavalents and octavalents also. Longley and Clark (1930) saw sporads with five or with six or more cells from one pollen mother cell, not the multivalents attributed to their results by Swaminathan and Howard (1953). Müntzing (1933) and Ellison (1936) interpreted the associations as evidence of a higher degree of polyploidy, the basic number being six, but the others interpreted them as products of segmental interchange. Lamm (1945) did not observe any association higher than four in any of the 4n species he examined.

In the cross of the tetraploid species (2n = 48) *Solanum acaule* × *S. antipoviczii,* Propach (1937) observed chromatin bridges, sometimes with a fragment, and considered them as evidence of translocation or inversion.

Violaceae—violet family.

Viola. Clausen (1931b) found associations of three, four and six chromosomes in hybrids between species in the Melanium section of *Viola,* and stated that some might indicate polyploidy, others probably indicated interchange.

MONOCOTYLEDONEAE.

Amaryllidaceae—amaryllis family.

Miersia. Cave and Bradley (1943) observed two types in *Miersia chilensis.* One had nine pairs of rod-shaped chromosomes plus a pair of V-shaped ones. The other type had 9 II of rods + one V and two rods. They suggested that a translocation process may have been involved, either in the formation of a V chromosome from two rods or vice versa.

Nerine. In *Nerine undulata,* one chromosome had a nucleolus at or near the centromere, possibly as a result of translocation (Battaglia, 1953). Sato (1942) observed that in this species the position of the secondary constriction was different from that in other species of *Nerine.*

Pancratium. In *Pancratium illyricum* the presence of chromosome knots and ring fragments at the post-meiotic mitoses was interpreted as the result of earlier structural changes (Husted, 1937). One published figure showed a reciprocal chromatid translocation.

Zephyranthes. In *Zephyranthes candida* (2n = 38), Nagae and Takusagawa (1932) observed that several chromosomes, usually four, six or eight, were arranged in a ring at metaphase. Although they did not suggest it, the higher associations might have come about, in part, through translocation.

Commelinaceae—spiderwort family.

Campelia. In this monotypic genus Anderson and Sax (1936) reported two chains of four chromosomes each plus 4 II in *Campelia zanonia.* No evidence of interchange was found by Simmonds (1954) in the material he studied.

Rhoeo. In the monotypic genus *Rhoeo discolor* (2n = 12) Belling (1927) reported that the chromosomes were sometimes united into a chain of V's, alternate chromosomes passing to opposite poles [24]. Darlington (1929a, b) reported a ⊙12 at diakinesis in about 30% of the cells: one chain of 12 or two or three chains with varying numbers of chromosomes in 45, 20 and 5% of the cells, respectively. About half the disjunctions were zigzag, according to Sax (1931), but irregular ones were more frequent

[24] The intention probably was to state that adjacent chromosomes passed to opposite poles.

than in *Oenothera*. Sax suggested this might be due to the translocations being more nearly terminal. The centromeres were median except for four, in which the shorter arm was less than half the length of the longer. He reported also that not all the chromosomes established their relationship with the spindle simultaneously. Other studies on *Rhoeo* have been reported by Kato (1930), Sax (1931), Koller (1932), Sax and Anderson (1933), Sax (1935), Anderson and Sax (1936), Straub (1936, 1941), Akemine (1937, 1947), Ellenhorn (1940), Bhaduri (1942a) and Simmonds (1945).

Collections from widely different sources have shown a ⊙12 as the maximum configuration (Simmonds, 1945). Anderson and Sax (1936) observed that the progeny bred true, supposedly by a system of balanced lethals. Straub (1941) reported a plant with ⊙8 + ⊙4 among the progeny. Sax (1935) reported that the meiotic chromosomes were always paired by terminal "chiasmata" and that pollen sterility was about 80%. Kato (1930) also reported that four of the chromosomes were hetero-brachial. Koller (1932) observed side-by-side pairing of chromosome ends at prophase I. Straub (1936) reported that low temperature (10° C. for 16 days) greatly decreased the association of the chromosomes, while high temperatures had no effect. In 1941, Straub reported parasyndesis of only the chromosome ends at pachytene. The presence of a paracentric inversion in the line he studied enabled him to measure crossing over frequency in that arm. At anaphase I, 25.3% of the cells had a bridge, while at anaphase II, 10.5% had a bridge. The latter result from simultaneous crossing-over in the inverted and not-inverted portions of the chromosome arm with the inversion. A high frequency of crossing-over in that arm is indicated. The general scheme he proposed was that the chromosomes have long differential segments proximal to the centromeres within which no cross-overs occur, then short crossing-over segments between them and the pairing end segments. The chromosomes were stated to be mostly euchromatic.

Akemine (1937) reported that non-disjunction of adjacent centromeres connected by two short arms was more than seven times as frequent as that when adjacent centromeres were connected by long arms. In 1947 he reported that four chromosomes could be distinguished from the others. Ellenhorn (1940) noted

differences in intensity of staining in the chromosomes; three slightly stained throughout, the others darkly stained in regions proximal to the centromere or one entire arm. No two chromosomes were alike. It was proposed that the presence of slightly stained and darkly stained regions in the same arm indicated translocation between two ancestral species which had once hybridized and which differed in stainability of their chromosomes. These differences have not been noted in other reports.

Bhaduri (1942) found two secondary constrictions and two nucleoli in somatic nuclei of *Tradescantia* which is a close relative of *Rhoeo*. In *Rhoeo* he observed eight secondary constrictions, each of which was considered to be a nucleolar constriction, although six nucleoli were the most observed in one nucleus. He concluded that the higher number in *Rhoeo* is due to successive translocations between nucleolar and non-nucleolar chromosomes.

Simmonds (1945) examined two collections of tropical material. Both had a ⊙12, but he reported a much higher frequency of nondisjunction than in earlier reports. It is not known whether this reflected genetic difference in stocks or differences in environment.

In a spontaneous tetraploid *Rhoeo discolor,* Walters and Gerstel (1948), observed chains with three to 12 chromosomes, rings with four to eight chromosomes and more complex configurations with multiple chiasmata. All the metaphase cells had more than one configuration, the average being eight separate ones, whereas in the diploid only 30% had more than one. There was a higher percentage of normal-appearing pollen than in the diploid, 73 vs. 33 per cent. This was ascribed to the greater tolerance of the pollen of the former for deviating chromosome numbers. The majority of the progeny of the tetraploid had aneuploid numbers. Aneuploids have never been reported in the progeny grown from the diploid. The 13-chromosome clone of Singh et al. (1940) was described as having its chromosomes "arranged in a circular ring" in a large number of cells. Interstitial chiasmata have never been reported in the diploid. Only two were found in the tetraploid.

Setcreasea. In *Setcreasea brevifolia* (2n = 24) there was a chain of eight chromosomes (Richardson, 1935). In *S. pallida* (2n =

36), associations of three, four, five and six chromosomes were observed (Celarier, 1955).

Tradescantia. In *Tradescantia edwardsiana* (2n = 12), Sax and Anderson (1933) reported an occasional plant with an association of four chromosomes. They were mostly chains. Closed rings were rare, but about 15% were " pairs ", indicating that relatively short pieces probably were exchanged. They reported a relationship between the kind of segregation from the ring and the relative frequencies of terminal and subterminal chiasmata in the interchange complex. In those with only terminal chiasmata there was a ratio of about two alternate : one adjacent; with one subterminal chiasma it was 1 : 1.2; with two it was about 1 : 1.8; and with three, all were adjacent (12 figures). For the total the ratio was about 1 : 1. Pollen counts showed 45.6% of imperfect pollen.

In *T. reflexa* (2n = 12) one plant was found with an association of four chromosomes. Rings were much more frequent than chains. One or more subterminal chiasmata were in 40% of the configurations. Adjacent chromosomes were directed to the same pole in 83% of the cells. Pollen abortion varied from 90% to almost zero on different days, but the general average was 35% not morphologically perfect.

A configuration of four chromosomes, a ring or a chain, was found in occasional plants of *T. humilis, T. canaliculata* and in *T. gigantea* (Anderson and Sax, 1936). They reported also two configurations with four chromosomes associated in the variety Victoria, an unidentified species of *Tradescantia* related to *T. gesneriana* (2n = 16).

In *T. bracteata* (n = 6) Darlington (1929a) reported a low frequency of meiotic divisions with four chromosomes associated. In *T. crassifolia,* association between two bivalents was found occasionally. It may or may not have been due to interchange. In *T. virginiana* (2n = 24), a polyploid, Miyake (1905) mentioned associated chromosomes. Multivalents with more than four were reported by Darlington (1932) and Koller (1932). For certain 4n species, a ⊙6 or a ⊙8 was observed by Anderson and Sax (1936). They were not certain that both were due to chromosomal interchange.

In *T. commelinoides* (2n = 14) Celarier (1955) reported a ⊙4 + 5 II in about 10% of the cells.

Tripogandra. In *Tripogandra pflanzii* (2n = 16), a ⊙4 + 6 II, and in *T. amplexicaulis* (2n = 16), there was a univalent, trivalent or a ⊙4 (Celarier, 1955).

Zebrina. In *Zebrina pendula* (2n = 24) there were two ⊙4 with chromosomes of unequal length (Darlington, 1929a). Plants examined by Simmonds (1954) did not have any translocations.

Cyperaceae—sedge family.

Carex. Wahl (1940) reported that usually in the cross of *Carex swannii* (n = 27) × *C. gracillima* (n = 27) there was an association of six or eight chromosomes and two groups of four. Although the chromosome number indicates polyploidy, reciprocal translocation was suggested as the explanation for the associations of more than four chromosomes, and also for the presence of chromosomes of unequal size in associations of three.

Tanaka (1946) summarized his cytological observations on a large number of species of *Carex*. In three species (2n = 60 or 62, 64) an association of six chromosomes was observed, supposed to be due to polyploidy and to translocation. In three other species there was complex structural hybridity with polyploidy and translocation.

Gramineae—grass family.

CEREALS

Aegilops—see *Triticum.*

Avena. Crosses of *Avena brevis* and *A. weistii* (both 2n = 14) with cc1795 (*A. strigosa?*) produced plants with a ⊙4 and 35% pollen abortion (Ellison, 1939). In the progeny two fertile types were isolated which, when crossed, again produced an F_1 with a ⊙4. One of these was homozygous for the interchange.

Ellison also reported a ⊙4 and 33% sterility in the cross of *A. barbata* × *A. abyssinica* (both parents were 2n = 28 and had only chromosome pairs). In a strain of homozygous fatuoids in *A. sativa* (2n = 42), Huskins (1925) reported at diakinesis 19 II plus a ring of four chromosomes, 17 II plus two rings; or configurations with three chromosomes. In a dwarf fatuoid produced by X-raying a dwarf line of *A. sativa,* Derick and Love (1937) observed two associations of four chromosomes. The parent dwarf

line had one such association. Nishiyama (1929) observed a tetrapartite configuration in *A. barbata* (n = 14) × *A. strigosa* (n = 7). In crosses between species with 21 pairs, *A. fatua* × *A. sterilis* often showed a ⊙4, while *A. sativa* × *A. byzantina* showed it only rarely.

Hordeum. In cultivated barley, *Hordeum vulgare* (2n = 14), Smith (1941) reported two translocations which occurred naturally. They differed greatly in the relative frequencies of ring, chain and pair configurations. For one there were 44.4, 41.9 and 13.6 per cent, respectively, of the three configurations; for the other, 5.3, 41.9 and 33.0. In the former translocation, 67.2% of the configurations were rings, in the latter 57%. These were later designated as translocations "A" and " B ". The former was used in a study of the application of the product method in the calculation of linkage intensities from F_2 data involving an interchange (Joachim, 1947).

A group of translocations produced by X-raying was reported by White and Burnham (1948) and by Burnham et al. (1954). By intercrossing and cytological examination of the F_1's a set of five tester translocations was established and used subsequently for determining the chromosomes involved in terms of the temporary letter designations a, b, c, d, e, f, g. Pollen abortion of the heterozygous plants averaged 25%, with a range from 14 to 58% in different lines. Seed set in many cases was lower than indicated by the pollen fertility. Of 35 translocations, 27 have been established in homozygous condition (Burnham et al., 1954). Linkages between partial sterility in certain of these translocations and characters in the different linkage groups appear in the above papers and by O. Smith (1949), Waddoups (1949), Hanson (1950, 1952), Hanson and Kramer (1949, 1950), Kramer (1954), and by Kramer, Veyl and Hanson (1954). In the latter paper linkage groups III and VII, which had been thought to be independent, were shown probably to be on the same chromosome, leaving at least one linkage group still to be identified. Identification of linkage group I with *f*, II with *a*, III with *b*, IV with *e*, V with *d*, VI with *c* and the missing group with *g* appears probable at the time of this summary, but tests are not complete. The linkage data with the translocations are sufficient to establish the independence of all the linkage groups except III, VII, and V;

II and IV (Burnham, in ms.). Only a *b–d* translocation has shown linkage with factors in V; an *a–e*, linkage with a factor in II. Chromosomes *a* and *d*, as well as *g*, may not have any known genetic markers.

According to Hagberg and Tjio (1950), Tjio and Hagberg (1951), Hagberg, Nybom and Gustafsson (1952), Hagberg (1954) and Gustafsson (1954), three of the "erectoides" mutants are inseparable from different translocations. In their 1950 and 1951 reports the morphologies of the chromosomes in somatic metaphase in root tips of "erectoides" translocation stocks were compared with those of normal stocks. In 1952, Hagberg and Tjio made similar studies on five of the translocations used by Burnham et al. and by Kramer et al. In two of them the new morphologies were sufficiently different, because of an exchange of pieces of unequal length, to permit identification of the chromosomes involved in terms of their chromosome idiogram, in which chromosomes 1 to 5 are in order of decreasing length, 6 has the larger satellite, 7 the smaller satellite. (Arabic numerals have been substituted here for the Roman ones). A study of new material (Burnham and Hagberg, in ms.) of the same translocations leaves little doubt that *b* is not 3 but may be 1 or 2, probably the former. Also *e* is 4, *a* is 5, *g* is 6, and *d* is 7. Smith (1950) reported on atom bomb effects on barley, and described mutants associated with translocations. Nybom (1954) reported complete linkage between an alboviridis mutant and a translocation. Moh, Nilan and Elliott (1955) observed a case in which all the partially sterile plants segregated yellow-green seedlings. It was interpreted as the result of insertional translocation. Translocations induced by X-rays have been used by Nishimura et al. (1952) and Nishimura and Kurakami (1953) in a program to build larger rings.

Moh and Nilan (1954) reported a translocation heterozygote in the progeny of X-rayed seeds of a recessive short chromosome stock.

Trisomics in the progeny of interchange heterozygotes were found by Burnham et al. (1954) and by Ramage (1955) and by Hagberg (1954). The trisomics first reported by Smith (1941) may have had their origin in the "A" or "B" interchanges seen by him, since one of those trisomic stocks is still segregating plants with a ⊙4 (Ramage, 1955).

Oryza. In fertile strains of rice, *Oryza sativa* (2n = 24), there were occasional semi-sterile plants (Terao, 1921, 1923). One plant bred true, another gave the typical 1 normal : 1 semisterile segregation, the latter continuing to segregate. Terao referred to Belling's case of semisterility but believed it would not explain his results. He assumed a lethal factor which caused the death of the ♀ gametes only.

Kondo and Ono (1924–25), Kondo (1927) and Kondo and Fujimoto (1927) described the breeding behavior of partially sterile rice plants in other varieties. An occasional one bred true but usually they segregated normals and partly steriles. Usually the fertile offspring bred true. It is probable that certain of the partially sterile lines were interchange types. Ishikawa (1927) reported several types of sterility in rice. A semisterile type was similar in breeding behavior to that of Belling's *Stizolobium.* Crosses between fertiles thrown by selfed semisteriles gave either all fertiles or all semisteriles. A two-factor explanation was offered. Ramiah (1931) also reported sterility in rice.

In hybrids between several varieties in the *Japonica* and *Indica* types (subspecies), J. W. Jones (1931) observed 52.6 to 83.6% of sterility based on seed set in the panicles. One hybrid had 28.9% of sterility. He observed segregation in F_2, but the numbers with different degrees of sterility were not given. Terao and Midusima (1939) also observed sterility in hybrids between the *Japonica* and *Indica* types and attributed it to segmental interchange, although they suggested also that it might be due to gene interaction or mutation. Hsu (1945) reported partial sterility in two crosses between the *Japonica* and *Indica* types. One had 59%, the other 77% of aborted pollen. The partially sterile plants always segregated, even into F_7; the fertile ones bred true. He assumed two factors, one of them being in the chromosome reported by Nandi (1936) to be present in four doses, the other in a disome. The interchange explanation seems simpler. Morinaga (1942) offered as an explanation of the sterility between *Japonica* and *Indica* types the excessive difference between the genes of the two subspecies resulting in a breakdown of genic balance in later generations.

Cua (1952), in his conclusions referred to several reports which attributed the observed sterility to segmental interchange, even in the absence of rings: Nakamura (1931), Kihara (1932), Morinaga

(1939). Cua (1952) noted higher seed fertility in tetraploids produced by doubling the chromosome number of the more sterile diploid hybrids. This would be expected with the translocation explanation.

Translocations have been produced in rice by X-rays (Ramiah et al., 1935; Parthasarathy, 1938; Nishimura and Kurakami, 1952). In a semisterile mutant from X-raying, Parthasarathy (1938) found an association of four chromosomes. Semisterile plants segregated semisteriles, normals and dwarfs in a ratio of 1002 : 667 : 273. The dwarfs had normal pollen but no seed set. It was suggested that they might be homozygous for the translocation, the abnormal phenotype being due to a small deficiency at or near one of the break points. He considered the segregation ratio as roughly approximating 2 : 1 : 1. My calculations show that the large deviations may be explained by a lower transmission of the translocation through the pollen. That might be expected from his assumption of a deficiency associated with the translocation. A " stumpy " mutant from the same line was trisomic and showed a chain of three or five chromosomes or a ⊙4 plus one univalent at meiosis. In a report by Oka et al. (1953), two lines from X-ray treatment showed partial sterility and an association of four chromosomes. In the progeny of one of them there was a ratio of 1 normal : 1 partly sterile plant. The degree of sterility was 50 to 60%. Only part of the cells showed the association of four chromosomes. Using data on the frequency of rings, chains and " pairs ", they proposed a formula for calculating lengths of interchanged segments, and the average lengths of the interstitial segments. Oka et al. stated that a greater part of the sterile rice plants after the Hiroshima and Nagasaki A-bomb exposure showed associations of four chromosomes. Reports on atomic bomb effects on rice have been published by Nagamatsu (1950) and Nishimura (1950).

Ramanujam (1937) observed an occasional association of six chromosomes in an autotriploid (36 chromosomes).

Morinaga (1934) observed one or two bivalents in haploid *O. sativa*. The associations found by Nandi (1936) were of the secondary type, not translocations.

Secale. In cultivated rye, *Secale cereale* (2n = 14), Darlington (1933) observed that a group of eight spore-mother cells in an

otherwise normal anther had a ⊙4 + 5 pairs. Müntzing (1939) found one plant with a ⊙4 + 5 II among 15 examined. Kostoff (1939a) reported that one member of a pair of twin seedlings had a ⊙4, the other only 7 II. Müntzing and Prakken (1941) reported that six plants of 167 in rye were heterozygous for interchanges, mostly a ⊙4, but that one had two ⊙4. According to them, zigzag orientations were much more frequent than open ones in the ⊙4. In the type with 2⊙4, the zigzag : open types were in a 3 : 2 ratio. In certain lines the configurations indicated that short segments had interchanged. Akdik and Müntzing (1949) reported a ⊙4 in a strain of rye from Ecuador. There was a ⊙4 + 5 II in the progeny of several partially sterile heads selected by Burnham from an increase field of the Emerald variety (Putt, 1954).

Kattermann (1939) described a new karyotype in inbred rye, in which one pair of chromosomes had a nearly terminal centromere. This was recognizable at anaphase I of meiosis. One proposed explanation was a translocation which transferred the centromere to the new position.

Schiemann and Nürnberg-Krüger (1952) reported that *Secale cereale,* crossed with *S. montanum* or with *S. africanum,* produced F_1's with 4 II + a chain of six or smaller chains. *S. montanum* × *S. africanum* had 7 II. Therefore the *Secale cereale* used differed from the wild species by two reciprocal translocations. Price (1955) also observed a chain of six or smaller configurations in hybrids between *S. cereale* and two strains of *S. montanum.*

In the second generation from hybrids between wheat and rye, there was an association of as many as six chromosomes (Kattermann, 1934, 1935a, b.)

Sorghum. In *Sorghum versicolor* (2n = 10) one line with a ⊙4 produced by X-ray treatment has been studied (Garber, 1948). There was a ratio of about 1 open : 1 zigzag orientation of the ring at metaphase I of meiosis. Pollen abortion in plants with a ⊙4 was 50.6%. In the normals it was less than 5%. Since the ring was associated with the nucleolus, it was possible to determine the chromosome behavior in the ring. By direct counts of the microspore quartets which had two adjacent spores with a diffuse nucleolus, there was 23.2% of adjacent-2 segregation. Using the pollen abortion counts, there was somewhat less than 26.8% of

adjacent-1, and about 50% of alternate segregation. This behavior is similar to that in maize.

Triticum, Aegilops. In *Triticum monococcum* (2n = 14), translocations produced by X-rays or other irradiations have been studied by Katayama (1935a, b), Smith (1936, 1938, 1939), Thompson and Thompson (1937), Thompson and Hutcheson (1942) and Yamashita (1947, 1950a, b, 1951, 1952a, 1953). Pathak (1940a) described an association of four chromosomes but interpreted it as being made up of chromosomes which were originally homologous. Pollen abortion in the plants with a ⊙4 is very low, the reports of Thompson et al. and of Smith indicating little increase over that in normal plants. Yamashita (1951) gives an average of 9.4% for those with a ⊙4 and 1.3% for the normals. Burnham et al. (1954) also reported similar low sterility, but that it is probably high enough under favorable conditions to permit identification of plants with a ring of four chromosomes.

Pollen abortion is greater in the larger rings (Smith, 1938, 1939; Yamashita, 1951). A high proportion of zigzag orientations was noted: 73% by Smith (1939) in the ⊙4; 88% in the ⊙4 and 75% in the ⊙6 by Thompson and Hutcheson (1942). Yamashita (1951) computed a mean of 82.7% for plants with a ⊙4, but only 22% for a ⊙12. Thompson and Hutcheson observed the configurations at pachytene and determined the relative lengths of the arms of the cross-shaped pachytene configurations in plants with a ⊙4, and in plants with different kinds of ⊙6, i.e., the ⊙6 in which both breaks in the common chromosome occurred in the same arm and the ⊙6 in which they occurred in opposite arms. They also established them as fully fertile homozygous lines, intercrossed them, and showed that in the seven lines with a reciprocal translocation, all but one chromosome was involved.

Yamashita (1951, 1952a, 1953) reported nine translocations in *T. monococcum* and seven in *T. aegilopoides* from X-irradiation, and the identification of the chromosomes of most of them in terms of an *a* to *g* designation for the seven chromosomes. Crosses between the translocations and successive crosses over an 11-year period established all the possible different combinations and sizes of rings, including a ring of 14. One homozygous stock which produced a ⊙6 when crossed with normal must have come from a

crossover in the differential segment in the chromosome common to two different translocations. The other stocks established produced separate rings of four when crossed with normal. Pollen fertility in the largest ring was only 12.5%. Seed set by hand pollination was 13.7%, but only 4% or less in heads that were bagged but not hand pollinated. In plants with the larger rings and the higher degrees of sterility, the anthers did not dehisce naturally but had to be torn apart.

Yamashita (1949, 1953) reported using translocations in determining the chromosome which carries a given gene, the establishment of the seven linkage groups in *T. monococcum* using X-ray induced mutants, and the plan to produce true-breeding translocation heterozygotes by introducing balanced lethals into the stock with the large ring.

Cytological examination served to classify the plants as to the presence or absence of the ring for use in linkage tests, but he suggested pollen classification as a more efficient method.

Also in *T. monococcum* Smith (1948) reported that in the progeny of a translocation heterozygote showing rings and chains, about seven per cent of the plants had a duplication plus deficiency. When this latter type of plant was crossed as ♀ with normal, 31% of the progeny were of that type (duplication + deficiency). When selfed, 39% had the duplication plus the deficiency. There was little or no transmission through the pollen. He presented data showing that the ratios for genes on the translocated piece or near the break on the non-translocated segment deviated greatly from normal ratios, thus demonstrating their usefulness in locating genes. Smith (1947b) also suggested using for linkage tests a translocation between a fragment and a normal non-homologue (lack of ♂ transmission).

Occasional complexes of three and four chromosomes were reported in crosses between 7-chromosome *Triticum* and *Aegilops* species of the Triticinae (Kihara and Lilienfeld, 1932, 1935a, b; Sears, 1941). Sears (1941) also recorded associations of five, six, seven and eight chromosomes in certain of the amphidiploids. These probably indicate the presence of interchanges.

Smith (1936) found a ring of four chromosomes in all the crosses involving *T. aegilopoides* var. *baidaricum* (n = 7). Four were with *T. monococcum*, varieties *flavescens, vulgare, pseudo-*

vulgare and *hornemanni*. Another was with *T. Ae. stramineo-onigrum*. In F_2 of each of the crosses there was a ratio of about 1 normal : 1 ring-forming plant. "Ring-forming plants did not have appreciably more aborted pollen than normal plants". In the ring from the cross with *T. monococcum* (var. *flavescens*) there was a ratio of about 2 open : 1 zigzag configuration at early metaphase, while at late metaphase it was about 1 : 1.2.

An association of three chromosomes (one with four) observed in some cells of *Aegilops ovata* (n = 14) × tetraploid (2n = 28) *Ae. bicornis*, and an association of three or of four chromosomes in *Ae. ovata* × *tetraploid* (4n) *Ae. squarrosa* were interpreted as associations between semihomologous chromosomes in different genoms (N. Kondo, 1946).

Tascher (1929) stated that sterility induced by X-raying dormant seeds was found in *Triticum monococcum* and *T. durum* but not in *T. vulgare*, probably as a result of the higher polyploidy. Sterile plants were common in *T. monococcum* but comparatively rare in *T. durum*.

Thompson and Thompson (1937) reported two translocations in *T. durum* (n = 14) produced by irradiation. These were stated to be nearly normal in fertility. Sizova (1939) found that two subspecies of *T. durum* (*abyssinicum* v. *gondaricum* and *expansum* v. *leucurum*) differed by a translocation involving one of the two chromosome pairs with a satellite. In the F_2 of the cross the two parental types with 14 II were found and also plants with 12 II plus a ⊙4 associated with the nucleolus.

There was an association of four chromosomes in every cell of a cross of *T. durum* (var. Kubanka) × *T. persicum* (both n = 14) (Smith, 1947a).

Hosono (1935) reported that in all hybrids in the Emmer series (n = 14) a few ⊙4, or 2⊙4 were observed, the highest frequencies being in *T. dicoccum* × *T. durum*, × *T. dicoccoides* and × *T. turgidum*, with 17.6 to 38.4% of the cells showing a ⊙4. In general the open rings were more frequent than zigzag; for all the crosses there were 230 : 96 or 29.4% zigzag configurations. Kihara and Lilienfeld (1932) reported a group of four chromosomes in the cross of two subspecies of *Aegilops ventricosa* (n = 14).

In a hybrid between *T. dicoccum* and *T. monococcum* Mather

(1935) found associations of four, four plus three, five, or five plus three chromosomes, indicative of structural heterozygosity.

Kihara and Lilienfeld (1948) reported multivalents in plants with doubled chromosome number from *T. turgidum* × *Ae. squarrosa* and *T. dicoccoides* × *Ae. squarrosa* hybrids (n = 14 × n = 7). Kihara and Matsumura (1941) wrote that in *Aegilops caudata* (n = 7) × *Ae. cylindrica* (n = 14) a reciprocal translocation resulted in variation in chromosome number in backcrosses to *cylindrica*. Hybrids between *Aegilops* and *Triticum* species with 2n = 14 chromosomes showed mostly univalents but a few bivalents in F_1 (Simonet, 1952). These F_1's, when crossed with *T. vulgare*, produced plants with an average of 17.5 bivalents and a few associations of three or four chromosomes. He pointed out that these associations offer the possibility for crossing-over between homologous-chromosomes.

Winge (1924) reported an association of three chromosomes in a heterozygous speltoid, and a configuration of four in the homozygous type. Huskins (1931) found a quadrivalent made up of two long and two short chromosomes in Vilmorin's unfixable dwarf wheat.

Camara and Rodrigues (1946) obtained evidence that γ speltoids may arise when the long arm of chromosome C is translocated to another chromosome, resulting in multiple associations at meiosis.

Sears (1939a, b) observed in the progeny from haploids (from the cross of *T. vulgare*, variety Chinese spring, × rye) pollinated by *T. vulgare*, two plants with a ⊙4. In one of the progeny from one of these, different configurations indicated that it may have come from a deficiency-duplication gamete.

Haploid plants from *T. monococcum* have been shown to have an occasional bivalent (Kihara and Katayama, 1931; Katayama, 1935c; L. Smith, 1946). Smith (1946) reported cytological observations on 30 diploid offspring of *monococcum* haploids. Seventeen of these had a ⊙4 + 5 II. In *T. durum* (n = 14) haploids Kihara (1936) found one bivalent fairly frequently, but three pairs were observed only once. In the *vulgare* (n = 21) haploids, Krishnaswamy (1939) reported that in 710 P.M.C. examined, 59.3% had 21 univalents, 38.8% had one to three bivalents, and only a few had a larger number of bivalents. Seven cells had a trivalent. McGinnis and Unrau (1952) reported that in a haploid

from the cross of Lemhi × (Bunyip × Dicklow) a large number of cells at meiosis had one to three pairs. The pairing in haploids indicates some homologies between different chromosomes in the haploid sets. Crossing-over between these homologous segments could produce translocations and is probably the source of the translocations found in the diploid offspring.

Person (1954) concluded that side-by-side metaphase-anaphase associations in the haploid indicated homology, but that no crossing-over had occurred. In addition there were bivalents with crossing-over.

Sears (1953) has asserted that certain varieties of *Triticum vulgare* (2n = 42) differ by a single translocation. In crosses with the variety Chinese Spring, the Thatcher variety was shown to differ by a translocation between chromosomes IV and X, the variety Indian by one between II and VII, and Poso (a variety of *T. compactum*) by a translocation between V and VII. He discussed the effect of the translocation on the end product of a series of backcrosses to Chinese nullisomics for the purpose of substituting one of these chromosomes in Chinese, also on the end product in transferring the nullisomic condition for one of these to a different variety. It appears to be much more difficult to accomplish than he has stated, since in either case the desired goal is dependent on crossing-over.

Morrison (1954) observed a translocation in *T. vulgare* involving chromosomes broken at the centromeres, believed to be misdivision of univalents in a monosomic plant followed by reunion in a new combination.

Ellerton (1939) found frequent multipartite configurations in hybrids between *T. sphaerococcum* and *T. vulgare* which he believed were due to interchange. Among the progeny in F_2, about one in 50 were speltoids. Camara (1945) saw such configurations in 33% of the cells in the F_1 of *T. vulgare* × *T. sphaerococcum*.

Love (1939, 1940) examined the vulgare-like derivatives of *vulgare* × *durum* wheat crosses. In 32 of the 50 lines there was evidence of chromosome aberrations, some of which were associations of four.

Kihara and Nishiyama (1930) reported translocations in hybrids between the different chromosome groups of wheat. Kostoff (1941b) met with associations of four or of three + a univalent or

two to four univalents in hybrids between 14 II wheat species, also between 21 II species, and between these and 21 II derivatives from 21 II × 14 II hybrids. The associations indicate structural hybridity which may have arisen by crossing-over between partially homologous chromosomes.

Matsumura and Nakamura (1943) reported a dwarf derivative of the cross of *T. polonicum* (2n = 14) with *T. spelta* (2n = 21) which, when crossed with the two parents, showed an association of four chromosomes. They concluded the dwarf was homozygous for a translocation.

There was evidence of interchange in the cross of *Aegilops triaristata* (n = 21) × *Ae. columnaris* (n = 14) (Nakamura, 1943).

A *T. vulgare* type extracted from a cross of *T. vulgare* × *T. monococcum* showed a chain of four chromosomes very often when crossed with a normal *vulgare* (Kostoff, 1937). He interpreted it as the result of crossing-over between two partially homologous chromosomes. Only one of the cross-over chromosomes was believed to be present.

In the progeny from backcrossing the F_1 of *T. vulgare* × rye with *vulgare,* some plants had a chain or a ring of six chromosomes, others a ring of four (Kattermann, 1934, 1935a, b). Up to four associations of four chromosomes were observed in two 42-chromosome plants which came from other wheat × rye crosses. These were speltoid heterozygotes which had weak hairiness (Kattermann, 1937).

Zea. The first section has included many of the findings on interchanges in maize, *Zea mays* (2n = 20). A few supplementary facts will be summarized here, together with a listing of most of the references.

At meiosis the hybrid of *Zea mays* (2n = 20) × *Tripsacum dactyloides* (2n = 40) showed one to six pairs of chromosomes, the pairing being weak (Mangelsdorf and Reeves, 1939). In the backcrosses to *Zea,* plants with 21 chromosomes, the extra one being from *Tripsacum,* were selected. Configurations of five and certain of those with three chromosomes were interpreted as being possibly the result of translocation or of crossing-over between partially homologous chromosomes.

The interchanges in maize have been recognized by the partial sterility they cause when heterozygous. There is no evidence thus

far that any of the lines in maize with a ⊙4 or a ⊙6 show directed segregation. The first interchanges were found in untreated material and were designated as semisterile-1, semisterile-2, etc. The breeding behavior of semisterile-1, as reported by Brink (1927) and Brink and Burnham (1929), was similar to that found by Belling for semisterility in *Stizolobium*. That is, the semisterile plants continued to segregate normals and semisteriles, whether selfed or crossed with normal; and the normals bred true. The rings of four chromosomes at diakinesis and at metaphase I of meiosis (Burnham, 1930), together with the cross-shaped configuration at pachytene (McClintock, 1930), established the fact that these were chromosomal interchanges. After the interchanged chromosomes were identified (see p. 433), the designation was changed to indicate the chromosomes involved, e.g., semisterile-1 became T1-2, i.e., a translocation between chromosomes 1 and 2. When a second one involving these two chromosomes was found, it became T1-2b, the first one T1-2a. Using the scheme first reported by Anderson (1938), the breakage points are given as proportions of the total arm length represented by the distance measured from the centromere to the center of the cross at pachytene, L and S being used to indicate whether the break was in the long or the short arm. For example, T8-10a is listed as 8L.68-10L.83, which means that the break in each chromosome was in the long arm, that in 8 being .68 of the distance from the centromere to the end of the long arm, etc. The lengths of the translocated pieces are one minus these values.

X-rays and other irradiations have been used to produce a large number of interchanges in maize (Anderson and Clokey, 1934; Anderson, 1935; Longley, 1950). Of the 90 interchanges with chromosomes identified as listed by Anderson (1935), only 14 had occurred naturally, the remainder being the result of X-ray treatment, except for one from the "sticky" chromosome character (Beadle, 1937). The first ones to be found were segregating in the stocks being used for genetic studies (Brink, 1927; Burnham, 1930; Rhoades, 1931). Several of the naturally occurring ones in Anderson's 1935 list were furnished to me by R. A. Emerson from his genetic stocks. In a survey of varieties and hybrids grown in a yield trial, Clark (1942) found that about one per 1,000 had transmissible partial sterility. Not all of these were

interchanges. Two of the inbred lines were homozygous for an interchange.

Blanco (1948) reported pachytene configurations that seemed to indicate heterozygosity for an interchange in certain lines. A naturally occurring one has been mentioned also by Menezes (1954). Alexander (1953) observed bridge-like configurations at anaphase I of meiosis in haploid maize. Translocations have been observed in their diploid offspring (personal communication).

Morris (1955) described the behavior of pseudoisochromosomes produced in X_1 by irradiating seeds (diploid tissue). They frequently lag at meiosis, but in some divisions both may pass to one pole. In many cases, the two arms were paired at pachytene beginning at the ends. The centromere was non-medial in certain of the published figures indicating that at least one of the two breaks was distal, not adjacent to a centromere. There was no information on the frequency of transmission to the offspring.

After the chromosomes in the first interchanges had been identified, those interchanges were used in intercrosses for identification of the chromosomes involved in new interchanges. Cytological examination for the number of rings present and the number of chromosomes in each furnished the necessary information, e.g., 2⊙4 or a ⊙6 were observed most frequently in the intercrosses. Tester sets were selected by Anderson, and by myself which would serve to identify the chromosomes involved in any new interchange. The tester set in use by the writer for chromosome identification for many years is the following: T1-2a, T2-4d, T3-7c, T5-7c, T8-9a, and T8-10b. Chromosome 6 is not included in these, but interchanges involving it are easily identified by their association with the nucleolus. A general scheme of selecting a tester set from a large number of interchanges, whose interchanged chromosomes have been identified, has been described by Burnham et al. (1954).

Using the method of pachytene analysis, Longley (1950) listed the chromosome identifications and the break points in 588 translocations. These included 179 from known dosages of X-rays, 172 from the Test Able A-bomb, and those from earlier X-ray treatments and other sources. This list, supplemented by information in the later Corn News Letters, furnishes the basic information which is available on the maize interchanges for use in planned

experimentation. With this basic information it is possible to make " studies on the chromosome mechanism in which crossing over statistics and cytological observations are intimately correlated " (Anderson, 1935).

The papers which present the general cytogenetic behavior of translocations in maize are the following: Brink, 1927; Brink and Burnham, 1929; Brink and Cooper, 1932a, b; Burnham, 1930, 1932a, b, 1934a, b, c, 1948a, 1950a, b; Clarke and Anderson, 1935; McClintock, 1930; Rhoades, 1931, 1933. Several of these reported linkage data between genetic markers and the semisterility caused by the interchanges. Unpublished linkage data from several workers with other interchanges are in the maize Linkage Summary (Emerson et al., 1935); also in the Maize Genetics Cooperation News Letters. Photomicrographs of the cytological configurations at meiosis in translocation heterozygotes may be found in papers by McClintock (1931b, 1932, 1933, 1934) and by Rhoades (1950).

Papers by McClintock (1931a) and by Burnham (1934c) reported the orientation of certain linkage groups and the positions of certain genes in relation to the translocation point. The orientation of the linkage group in each of the ten chromosomes is now known, many of them as a result of the linkage tests with translocations combined with the pachytene analyses.

Papers by Anderson (1938, 1939, 1941), Anderson and Brink (1940), Anderson and Kramer (1954), Anderson, Kramer and Longley (1955a, b) established the breakage positions of a series of interchanges involving the same chromosome in relation to genetic markers in the linkage map: in chromosome 9, 14 interchanges; chromosome 8, nine interchanges; chromosome 1, eight interchanges in the short arm; chromosome 3, 21 interchanges; chromosome 10, 18 interchanges; chromosome 4, 33 interchanges, and chromosome 6, 25 interchanges. A paper by Anderson and Randolph (1945) presented evidence for the location of the centromere in each of the linkage maps. For the method, see page 455. Patterson (1952) studied gene locations in relation to the cytological break positions in 18 interchanges which were identified by Longley as having their break points in the short arm of chromosome 9; also 17 which were in the short arm of chromosome 2 or were near the centromere. For the former group he reported a

special method of determining the position of the break with respect to the waxy gene and the centromere of chromosome 9 (see page 456).

An interchange with one break in the nucleolus attachment region produced two new chromosomes, each of which had a functional nucleolus-organizing region (McClintock, 1934). It formed a ring of four chromosomes. Anderson (1934) reported that most of the plants heterozygous for that interchange had about 50% of visibly abnormal pollen, but that there were some plants with about 25%. In the latter the normal-appearing pollen grains differed markedly in size, the smaller ones supposedly being those deficient for the segment including the satellite plus a portion of the organizer region.

Interchanges in which one of the exchanged pieces was a portion of the satellite produced a chain of four chromosomes at meiosis in the heterozygote. Sterility was about 25% (Burnham, 1932a; Clarke and Anderson, 1935).

There is considerable association of non-homologous parts at pachytene in regions near the breaks, as indicated by a lack of constancy in the position of the center of the cross-configuration (McClintock, 1932, 1933; Burnham, 1932b). This appears to decrease crossing-over (Burnham, 1934a, b).

The relation between genetic crossing-over and chiasma frequency in an interstitial segment which could be recognized in an interchange heterozygote was studied by Beadle (1932a) in a cross between *Euchlaena* and a maize interchange. There seemed to be an agreement in one case between the observed and the expected, but the chiasma frequency varied greatly from plant to plant, and genetic data from the different plants were not available. More data of this type are needed.

Two experiments using translocations in maize demonstrated that when a genetic cross-over has occurred there has been an exchange between the chromosomes: Creighton and McClintock (1931), using the terminal knob on chromosome 9 and T8-9a as markers; Cooper and Brink (1931), using genetic markers in the differential segment in a ⊙6.

The factors affecting chromosome segregation in rings of four chromosomes have been studied by McClintock (1934 and unpublished) and by Burnham (1945, 1949, 1950a, b, 1953), using

interchanges involving chromosome 6 in which non-disjunction for the nucleolus-organizer region results in recognizably different spore quartet types. See p. 447. A few data on variation in frequency of crossover quartets were obtained by Whalen (1951).

Rings of six chromosomes having greatly different pachytene configurations were planned by intercrossing different interchanges in an attempt to influence the degree of sterility. No marked differences were observed (Frolik, 1948; Frolik and Burnham, 1950).

The effect on crossing-over when low temperature was applied at various stages of growth was studied by Khan (1947, 1955), counts being made on the frequency of "cross-over type" spore quartets in plants heterozygous for an interchange with a break in the short arm of chromosome 6 (T5-6c). Low temperature during the development of the kernels had no effect on crossing-over in the resulting plants. The same was true for dry seeds and germinating seeds placed in the cold for 15 days. Growing plants were subjected to low temperature for periods from one to seven days duration at various stages. Plants subjected to 36 to 38° F. for six to seven days during the fourth week of development, for five to seven days during the fifth week, for three to five days during the sixth week, and four days during the seventh week showed the greatest increases in frequency of cross-over quartets, the observed values being usually above 60% as compared with 54.6% at normal temperatures. By the eighth week of development "meiosis in the tassel had almost finished". Exposures during that week gave no increases in crossing-over. There was no effect on crossing-over at 50° to 52° F. at any of the stages of development.

The behavior and uses of interchanges between the supernumerary, or "B", chromosomes and the primary ones have been reported by Roman and Ullstrup (1952). The points of interchange were easily recognized if the break in the "B" were in a heterochromatic region. When a line having a ring of eight chromosomes produced by X-raying a stock homozygous for one interchange is crossed with normals, the progeny include an occasional plant with a ⊙4 or a ⊙6 (Lazaro, 1944; Marino, 1947). For each of these smaller rings there are two types, each with a different combination of chromosomes. Pachytene analysis has

given a plausible explanation for the origin of these types by crossing-over (Mohamed, 1953).

Areas of irregular growth, both depressions and outgrowths, on the surfaces of maize kernels were noted by Jones (1937, 1938, 1944), translocations in endosperm tissue being suggested as the cause.

By using interchanges as markers, the chromosome arms which carry genes for smut resistance in certain inbreds have been located (Burnham and Cartledge, 1939; Saboe and Hayes, 1941; Saboe, 1942). These have been shown to be different in different resistant inbred lines. The gene for *Helminthosporium carbonum* resistance has been located in chromosome 1 (Ullstrup and Brunson, 1947) by this method. Interchanges were used for a study of the inheritance of oil content (Miller, 1951a, b), his conclusion being that it was complex. All the interchanges in the *su* series showed association, suggesting a linkage of at least one of the genes with *su*. At least three genes for the resistance of one inbred line to the European Corn borer were located by the use of interchange markers (Ibrahim, 1954). They have been utilized also in a study of pericarp tenderness in a sweet × field corn cross (Mohamed, 1954).

Their use to permit comparison of the characters carried by the translocated vs. the corresponding normal chromosomes, i.e., to control the chromosomes, has been suggested and used by Anderson (1952). It was employed also by Blanco (1950) in a study of pollen size variation; by Teas et al. (1952) in a study of the biochemical constituents of sugary and starchy maize kernels. This is the basis for the " Oenothera " method of producing inbred lines, as suggested by Burnham (1946).

Intercrosses between interchanges involving the same two chromosomes but with different breakpoints have been studied to determine the behavior of the expected deficiencies and duplications (Gopinath, 1950; Gopinath and Burnham (in press); Borojevic, 1954). Pachytene configurations were observed with loops or humps in one member of the pair. These configurations are expected when one chromosome is longer than the other. Borojevic observed pairing between the loops in the two separate " pairs ". Tests of two different crosses gave results indicating that a deficiency had functioned (Gopinath, 1950).

Tertiary trisomics were reported in the progeny of interchange heterozygotes (Burnham, 1930, 1934a, 1948a). The two types expected from one interchange, T5-6a, were established by Ibrahim (1950a, b). The two could be distinguished cytologically by the number of chromosomes attached to the nucleolus, by counts of the number of nucleoli in the microspores, and distinguished from the interchange trisomics by the absence of the T5-6a ring in their progeny.

The effects of atomic bomb irradiations on maize have been reported by Anderson et al. (1949), Randolph et al. (1949) and Randolph (1950).

The behavior of rings in maize as compared with those in *Oenothera* has been considered by Brink and Cooper (1932c), Emerson (1932) and Burnham (1950b).

Brief reviews on interchanges in maize have been published by Anderson (1936), Rhoades and McClintock (1935) and Yarnell (1954). Kachidze (1934) reviewed the published papers on translocations and other chromosomal changes in maize (in Russian).

Other Grasses

Agrostis. In *Agrostis nebulosa* (2n = 14), Tinney (1936) found in relatively few cells two or three bivalents attached at their ends at diplotene, diakinesis and metaphase I. He assumed these were the result of interchange. The small amount of aborted pollen was probably no different from that in normal plants.

Alopecurus. Johnsson (1944) reported sterility and meiotic abnormalities in *Alopecurus myosuroides* (2n = 28) and discussed the absence of translocations in plants of this cross-pollinated grass. She stated "The diploid and tetraploid species of *Alopecurus* represent two types with regard to chiasma morphology. At I-M one type has completely terminal chiasmata, the other is entirely non-terminalizing". *A. myosuroides* is one of the latter. Comparative studies of translocations produced experimentally in the diploid species should be of interest in relation to the problem of what determines chromosome orientation in rings. In *Alopecurus pratensis* (2n = 28), Rancken (1934) found a chain or a ring configuration in seven of 78 pollen mother cells. In one there was a chain of six chromosomes.

Anthoxanthum. Kattermann (1930, 1931) reported configura-

tions in *Anthoxanthum odoratum* (2n = 20) that varied from 10 II to a configuration of 12 chromosomes + ⊙4 + 2 II. Variation was observed in the same slide, including a group of 10 + ⊙4 + 3 II and various combinations of ⊙4, ⊙6 and pairs. Similar observations were made by Parthasarathy (1939) at meiosis. From observations on somatic divisions he concluded there were four sets of chromosomes, indicating tetraploidy, and that the higher associations were a result of interchanges.

Brachypodium. A ⊙4 + 12 II in *Brachypodium pinnatum* (2n = 28) was observed by Katterman (1930).

Briza. In 14 plants of *Briza media* (2n = 14), a perennial grass, Kattermann (1930, 1933, 1938a, b) found four with a ⊙4. In this species terminalization of subterminal chiasmata occurs. A count of clearly disjunctional : non-disjunctional figures showed an average of about 1 : 3. Seed-setting on one plant with a ⊙4 was 73.8%, in another 25.6%, while plants with 7 II varied from 20.5 to 69.2%. He also intercrossed a number of plants, including some with 7 II. One combination of the latter gave a semisterile F_1, showing that there were two kinds of homozygotes in the collections.

Dactylis. In *Dactylis aschersoniana* (2n = 14), of three plants examined, one had a segmental interchange (Müntzing, 1937). Seven pairs were observed most frequently. When associations were found, there was usually a chain of four chromosomes, occasionally a ring, also occasionally a III + I. Pollen sterility varied, but the average was 47%. Counts showed 38 zigzag : 26 non-disjunctional figures.

Eleusine. In *Eleusine coracana* (2n = 36, a polyploid), an occasional ⊙4 was observed by Krishnaswamy (1940). This may have been a result of the polyploidy, not of interchange.

Elymus. In *Elymus glaucus* (2n = 28), hybrids between different morphological strains collected at different locations in California showed associations of chromosomes (Snyder, 1951). Of 22 hybrids, ten had a ⊙4 + 12 II, two had 2⊙4 + 10 II. In three of them all the cells showed the ring, in the others only part of them did, the other cells having mostly 14 II. Pollen fertility in per cent in four hybrids was 73, 71, 23, 47, and on eight more was less than 1%. The cytology of the plants with 47%, 23% and one of the F_2's with 0% fertility indicated about 1N : 1 zigzag

orientation. In only four of the hybrids could all the pollen abortion be explained by the frequency of visible meiotic abnormalities.

In the cross of *Elymus canadensis* with *Agropyrum caninum* (both with 2n = 28) about 50% of the cells at meiosis had 11 to 13 II and six to two univalents, while the other 50% had one or two III, a IV, or a IV plus one or two III (Cugnac and Simonet, 1952).

Stebbins, Valencia and Valencia (1946) reported that all the hybrids of *Agropyron pauciflorum* with *A.* sp. "San Benito", *Elymus glaucus* and *Sitanion jubatum* formed associations of three, four, five and six chromosomes. The multivalents higher than four and the kinds of associations were evidence of interchange.

Hybrids of *Elymus condensatus* with *E. triticoides* (allopolyploids) showed some associations of three and four chromosomes which were interpreted as due to structural hybridity for a segmental interchange (Stebbins and Walters, 1949).

Festuca. Rancken (1934) found an association of four chromosomes in *Festuca pratense* (2n = 14), usually in an open configuration, rarely a ring. No observations on pollen abortion were reported. In the F_1 between *Lolium perenne* (n = 7) and *Festuca pratensis* one plant had a chain of four chromosomes in 4.8% of the cells (Peto, 1933). This was interpreted as the result of an interchange in one of the parents.

Pennisetum. In *Pennisetum typhoides* (2n = 14), Krishnaswami and Ayyangar (1941a, b) produced by X-ray treatment four plants with a segmental interchange. They had rings or chains in only part of the cells at meiosis. In an autotriploid they observed associations of five, seven, and ten chromosomes which were considered to indicate segmental interchange.

Puccinellia. Flovik (1938) found one association of four in a plant of *Puccinellia vahliana* (2n = 4).

Hydrocharitaceae—frogbit family.

Vallisneria. In *Vallisneria spiralis* (2n = 20), Winge (1927) observed that two pairs of chromosomes were united in a "double chromosome" at meiosis. The meaning is not clear, but it may indicate a translocation.

Iridaceae—iris family.

Crocus. Darlington (1937, p. 160), observed a group of 4 chromosomes plus 2 II in *C. chrysanthus* (2n = 8). In *C. susianus* (2n = 12) Pathak (1940b) found 4 II plus a group of four chromosomes; but believed that the latter were homologues due to duplication of one pair of chromosomes; i.e., the plant was tetrasomic.

Liliaceae—lily family.

Allium. In *Allium ammophilum* (2n = 16), an association of four chromosomes as a ring or chain or a III + I was seen from pachytene to anaphase I (Levan, 1935). Only about 25% of the chiasmata in the interchange complex were terminal. The ring was seldom oriented as a zigzag. One plant of *Allium cernuum* showed an association of four chromosomes in a ring, or less frequently in a chain (Levan, 1939). Zigzag and open configurations were about equally frequent, and pollen abortion was about 50%. This species with its chromosomes of about equal size, with median centromeres and high terminalization is an apparent exception to the rule that species with these features have regular zigzag orientation in interchange configurations.

In *Allium schoenoprasum,* a diploid, one case of translocation was reported, as judged by a different chromosome morphology in about half the pollen grains (Levan, 1936b). In *A. alleghenienense,* Levan (1932) noted fragments in certain plants. In one, a fragment was attached medially to one of the large chromosomes. He believed it was a translocation.

One strain of *Allium scorodoprasum* var. *viviparum* (2n = 16) showed associations of four, eight, or four and four, four and six chromosomes which must have resulted from translocations (Katayama, 1936). In the hybrid of *Allium cepa* × *A. fistulosum,* occasional associations of three, four or six were observed by Levan (1936a, 1941). These had not been seen by Emsweller and Jones (1935, 1945) in the F_1's of their crosses, using different varieties, indicating that the parental material used by Levan was structurally different from that of Emsweller and Jones.

Aloe. Darlington (1936) mentions that interchange heterozygotes had been found in *Aloe sisalana* by Frankel, Doughty and Darlington (unpublished). See below for hybrid with *Gasteria.*

Brodiaea. In *Brodiaea lactea* (2n = 21 to 24 pairs), propagated

by offsets from an underground corm, F. H. Smith (1933) observed in different cells a ⊙4 small chromosomes, a ⊙4 large ones, a ⊙4 large + a ⊙4 small, ⊙6, or ⊙6 + ⊙4 small. Cross-shaped configurations for the ⊙4 small chromosomes suggested an interchange. The ring of four large ones was believed to be due to two chiasma failures in the ⊙6. The chiasmata were usually terminalized before or during diakinesis. In most cases, adjacent chromosomes moved to opposite poles. The pollen from the one plant examined was morphologically perfect.

Fritillaria. Darlington (1936) stated that interchange heterozygotes had been found in ***Fritillaria dayphylla*** by Frankel, Doughty and Darlington (unpublished).

Gasteria. In *Gasteria gracilis* var. ***minima*** (2n = 14) a chain of four chromosomes was reported by Sato (1942).

In a hybrid of *Aloe variegata* × *Gasteria verrucosa,* both 2n = 14, about 1% of the cells had an association of four chromosomes (Sinoto, 1940; Sato, 1942). Also in *Aloe variegata* × *Gasteria gyuzetu* there was an association of three and a univalent in more than 10% of the cells.

Lilium. In *Lilium hansonii,* Haga (1938, 1943) reported a ⊙4 + 10 II, in which the major parts of both long arms were exchanged. The homologous centromeres remained synapsed up to anaphase I in the bivalents and in the ring. He stated that " only unbalanced pollen will be resulted as the two adjacent chromosomes paired by kinetochores pass to the same pole ". The meaning is not clear, but the published metaphase figures indicate he probably referred to adjacent-1 segregation. For these plants, pollen sterility was 99.8%, while for normals it was only 5.4%.

Nothoscordum. Levan and Emsweller (1938) reported that one form of *Nothoscordum fragrans* had 19 somatic chromosomes, four of which most commonly were in a ring and three in a chain made up of one median plus two telocentric chromosomes. The pairing conditions in the ring suggested an interchange. The ring was often a zigzag at metaphase.

Paris. According to Geitler (1938), inversions in *Paris quadrifolia* were the main structural abnormality, but five figures were explainable on the basis of simple translocation, two chromosome pairs being united. Husted (1937) noted knot configurations at the post meiotic mitoses in this species also.

Haga (1937), in the karyotypes of *Paris hexaphylla,* both in the diploid (2n = 15) and in the triploid, reported differences which he attributed to "simple translocation". There was frequent spontaneous breakage and fusion of chromosomes in the microsporocytes of *Paris verticillata* (2n = 10), and one published figure showed an interchange between the chromatids of two bivalents (Haga, 1953).

Polygonatum. Plants from the cross of *Polygonatum officinale* (2n = 20) × *P. multiflorum* (2n = 18) had 8 II plus a group of three chromosomes (Therman, 1953). She suggested that the decrease in number in *multiflorum* had been the result of unequal interchange, followed by loss of the smaller chromosome thus produced.

In one strain of *P. verticillatum* (2n = 28) there was an association of four chromosomes in most of the first metaphase plates (Therman, 1953b).

Scilla. In *Scilla,* Gopal-Ayengar (1942) reported the presence of inversions and translocations in several species, but the species names were not given. In *Scilla permixta* and in *S. ughii* Sato (1942) observed occasionally a tripartite configuration made up of chromosomes whose differences in length and morphology were ascribed to translocation. In these plants the chromosome number was 15, although plants with other numbers were observed also: 2n = 14 and 16 in *S. permixta;* 17, 19 and 20 in *S. ughii.*

Trillium. In *Trillium kamtschaticum,* one collection of 23 plants had two translocation heterozygotes (Matsuura and Kurabayashi, 1951). In 1948 Matsuura had reported two translocations in this same species. He identified the chromosomes involved and noted that equational and reductional separations of the centromeres were equally frequent. In 1950 he stated that parts of two chromosome arms had exchanged in one of these translocations; entire arms exchanged in the other.

Tulipa. In *Tulipa gesneriana* (2n = 24), Upcott (1937) found in each of two varieties two single chromosomes which differed from each other and from all the other chromosomes. Also these two chromosomes were different in the two varieties, indicating structural change, possibly translocation or inversion. In *T. orphanidea* (2n = 24) there was an association of four at pachytene

and at metaphase, in *T. praecox* (2n = 36, a triploid) a configuration of six chromosomes.

Musaceae—banana family.

Musa. Dodds (1943) reported that of five edible diploid parthenogenetic bananas studied (2n = 22), three were complex structural hybrids, showing multivalents, chromosome lagging, inversion bridges and high sterility. One had one reciprocal translocation, was semisterile in the pollen, and had highly sterile ♀ flowers. Dodds and Simmonds (1949) refer to "interchange hybridity" as an added source of sterility in *Musa.* Also see Simmonds (1955). Chakravorti (1951) reported that many varieties showed an association of four chromosomes. His illustrations showed a ⊙4 in three triploids.

Naiadaceae—

Najas. In *Najas marina* (2n = 14) Winge (1927) reported that two pairs of chromosomes were united in a "double chromosome".

Strelitziaceae (Musaceae)—

Strelitzia. In *S. augusta* (2n = 22) an association of four chromosomes was observed at metaphase I in 96% of the cells (Simmonds, 1954). There was alternate arrangement in 24% of the cells, and 34% of normal-appearing pollen.

GYMNOSPERMS

Taxaceae—Yew family.

Taxus. In *Taxus cuspidata* (2n = 24) the male plants examined at meiosis showed 10 II plus an association of four chromosomes (Matsuura and Suto, 1935).

Cephalotaxus. In *Cephalotaxus drupacea,* Sugihara (1940) reported that cytological observations on 34 trees showed five types: 12 II, 10 II + ⊙4, 8 II + ⊙4 + ⊙4, 7 II + ⊙4 + ⊙6, and 5 II + 2⊙4 + ⊙6. Of the figures for the ⊙4 and ⊙6, seven were zigzag and one open.

FUNGI

Ascomycetes

Aspergillus. In *Aspergillus nidulans,* Pontecorvo et al. (1949) mention that "an insertional translocation" was present in one strain.

Neurospora. In *Neurospora crassa* (n = 7), McClintock (1945) reported that three irradiation-induced mutants carried an interchange. In one of the stocks, a ring or a chain of four chromosomes or two "bivalents" were observed, in another a ring of four, or one or more univalents; while in the third the pieces exchanged appeared to be very unequal, one break close to the end of one chromosome, the other near the centromere. In this latter interchange heterozygote, by observing the unbroken 8-spored asci and determining the number and positions of the normal and the aborted or abnormal spores, she was able to study chromosome segregation in relation to the presence or absence of crossing-over in the interstitial segments. Based on her published data, 43.8% of the asci were recognizable as having crossed over in an interstitial segment (Type II ascus). The observed frequencies of Types I, III and IV asci were 197, 198 and 93 [25], respectively. If these came from meiocytes having no crossing-over in the interstitial segment, they would have come from alternate, adjacent-1 and adjacent-2 segregations, respectively. The data are very similar to those for this type of interchange in maize, the "no diffuse" and "two diffuse" spore quartet classes corresponding to the Type I and Type III asci. These three translocations in *Neurospora* and two more were studied by Singleton (1948). The chromosomes involved and the probable breakage points were determined for four of them. Linkages and pseudolinkages with these translocated stocks served to identify certain chromosomes with their linkage groups. He distinguished six kinds of asci, depending on the kinds of spores and their order. He developed formulas and methods for analyzing interchanges having both interstitial segments long enough to permit crossing-over. Counts were made on the frequencies of the different spore types, and an attempt made to apply the formulas. He considered the data unsatisfactory due to differential rates of maturity and consequent differences in ease of breakage of the asci as as they were being manipulated for counting of a non-random sample. In one interchange heterozygote, he observed a non-random distribution between ascus subtypes which differed only in spore position relative to the basal or apical end of the ascus, about a 2 : 1 ratio in place

[25] McClintock pointed out that the frequency of type III was probably too high since they were more resistant than the other types to breaking of the asci in making the slides.

of the expected 1 : 1. There was no evidence of directed segregation in *Neurospora,* either in McClintock's studies or in Singleton's.

Mitchell et al. (1952) and Pittenger (1954) studied the origin and behavior of pseudo-wild types [26] in F_2 of crosses between two linked recessives, when one was carrying a translocation and when both were normal. In the former report, both recessives were transmitted by the pseudo-wild types from the normal cross, but only one was transmitted by those from the translocation cross. There was a much higher frequency of pseudo-wild types from crosses involving a translocation. This is consistent with their explanation that pseudo-wild types are disomic and arise by nondisjunction, a relatively infrequent phenomenon in normal stocks but much higher in translocation heterozygotes. If the disomic nuclei functioned in the outcross to normal, both mutants should have been transmitted by each pseudo-wild type line. Since only one mutant was transmitted, it was assumed that the extra chromosome had been lost from the functional nuclei.

Yeast. Ranganathan (1950) described the change from diploid to top yeasts induced by temperature shocks and regarded it as the result of translocations. It would seem that more evidence is needed.

SUMMARY

The foregoing survey of the literature shows that translocations are of wide-spread occurrence in plants. Most of them have been found in the angiosperms: in 49 genera of dicots and 47 genera of monocots; but some have been reported in the gymnosperms (in two genera), also in the fungi. Studies at meiosis will undoubtedly reveal translocations in many other species, either in occasional plants or in different groups isolated geographically. In certain cases they seem to have played a part in the evolution of present karyotypes. In a number of cases, the presence of translocations has not been definitely established, but they are one possible explanation of the observed configurations.

The survey reveals the need for additional detailed studies of interchanges. What accounts for directed segregation in the interchange rings in certain species? For each of the factors which has been suggested there is one or more species which does not

[26] Wild types that were not due to recombination between the two loci.

behave in the predicted manner. Experimentally produced interchanges in other species having these features would be useful; also in species having directed segregation of the sex chromosomes. A discussion of how they have been and how they might be used as tools in the investigation of other cytological and cytogenetic problems and also certain applications to practical breeding have been included.

ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to Dr. L. A. Snyder for many helpful suggestions; to Dr. A. O. Dahl for checking the family names as used here; and to Mr. M. Tabata for translating several of the papers in Japanese. Thanks are due the personnel of the libraries at the University of Minnesota for their diligence in locating foreign and other publications. Indirect aid through Graduate School Research funds is acknowledged also.

The writer realizes that there are undoubtedly contributions on translocations in plants which he has overlooked. He will appreciate it if these are called to his attention, along with any errors of statement which may need correcting.

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Note added to galley (July 10):

Two papers have appeared since this was written: Thompson, J. B. and H. Rees, 1956. Selection for heterozygotes during inbreeding. Nature 177: 385–386. Thompson, J. B. 1956. Genotypic control of chromosome behavior in rye. II Disjunction at meiosis in interchange heterozygotes. Heredity 10: 99–108. The latter presents data purported to show that disjunction is genotypically controlled in rye.

Overlooked: Camara, A., D. Castro and M. Noronha. 1954. Two X-ray induced translocations in "*Luzula purpurea*." Genetica Iberica 6: 1–18.

* Publication not seen.

** Translated by M. Tabata.

Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

Fixation of Plant Chromosomes: Principles, Limitations and Recent Developments	A. K. Sharma *Calcutta University*
Reproduction in the Bangiophycideae	Kathleen M. Drew *University of Manchester*
Colonization of Artificial Bare Areas by Microorganisms	Wm. Bridge Cooke *Dept. Health, Education and Welfare* *Cincinnati, Ohio*
Recent Trends in Palynology	Knut Faegri *Botanisk Museum* *Bergen, Norway*
Cytoplasmic Male Sterility	John R. Edwardson *Agricultural Experiment Station* *Gainesville, Florida*